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ON SUBMICROSCOPIC STRUCTURE OF THE NAUTILUS SHELL,

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(With 8 Textfigures, 2 Tables and 24 Plates.)

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I. — INTRODUCTION.

In the literature on the structure of the nautiloid shell (Owen, 1832; Valenciennes, 1841; Carpenter, 1847; Edwards, 1849; Barrande, 1857; Keferstein, 1865; Waagen, 1867-1870; Hyatt, 1872; Nathusius von Königsborn, 1877; Blake, 1882; Brooks, 1888; Appellöf, 1893; Griffin, 1900; Willey, 1902; Pompeckj, 1912; Naef, 1921; W. J. Schmidt, 1923-1924; Bøggild, 1930; Teichert, 1933, 1934; Ahrberg, 1935; Flower, 1939; Miller, 1947; Mutvei, 1956, 1957; Moore, Lalicker and Fischer, 1952; Miller, Furnish and Schindewolf, 1957; Stenzel, 1957), substantial information has been obtained with the conventional light and polarisation microscopes.

The data so far collected on this structure with the electron microscope concern only the nacreous conchiolin of the inner layer of the shell wall in *Nautilus macromphalus*. This substance consists of lace-like reticulated sheets (Grégoire, Duchâteau and Florkin, 1950, 1955). The sheets belong to the system of organic membranes which run as continuous formations between the stratified mineral lamellae of mother-of-pearl and in each lamella, between the crystals of aragonite (Grégoire, 1957).

On the basis of these observations, nacreous conchiolin, with its texture more or less preserved, could be detected in fossil shells of cephalopod (ammonites, nautilids), gastropod and pelecypod mollusks (Grégoire, 1958, 1959 a b, and unpublished results). Small fragments or dust of crushed shells could be identified, at least at the class level, by recording with the electron microscope the pattern of structure of their nacreous conchiolin.

The present paper is an investigation on mineral and organic components of the *Nautilus* shell and on their relationships in the shell structure. The information obtained has already been used in the study of fossil nautiloid shells. The results will be reported elsewhere.

II. — MATERIAL AND METHODS.

The material used in the present study consisted of several dried shells of *Nautilus macromphalus* SOWERBY and of *Nautilus pompilius* LAMARCK, of dried remnants of soft parts (organic sheets from the convex side of the septa and from the area of attachment of the shell muscles), collected from these shells, and of a membrane, removed from the convex side of a septum in the anterior part of the phragmocone of a specimen of *Nautilus pompilius*, presumably fixed in alcohol immediately upon capture, kept in U. S. National Museum (635150), and kindly supplied by Dr. C. TEICHERT.

The preparations consisted of :

a) fragments of the outer and of the inner layers of the shell wall, fragments of the convex and of the concave sides of various septa, decalcified by chelation (saturated aqueous solutions of the disodium salt of ethylene-diamine tetra-acetic acid, pH 5,4 : sequestrene NA2, Alrose Chemical Corporation, Providence, Rhode Island, U. S. A.; titriplex III, Merck, Darmstadt (Germany) and exposed (in distilled water) to ultrasonic waves (1), in order to cleave the organic remnants into thin sheets permeable to the electrons. Parts of the organic material were immersed before the ultrasonic treatment in a 2 per cent aqueous solution of osmium tetroxide for 24 hours.

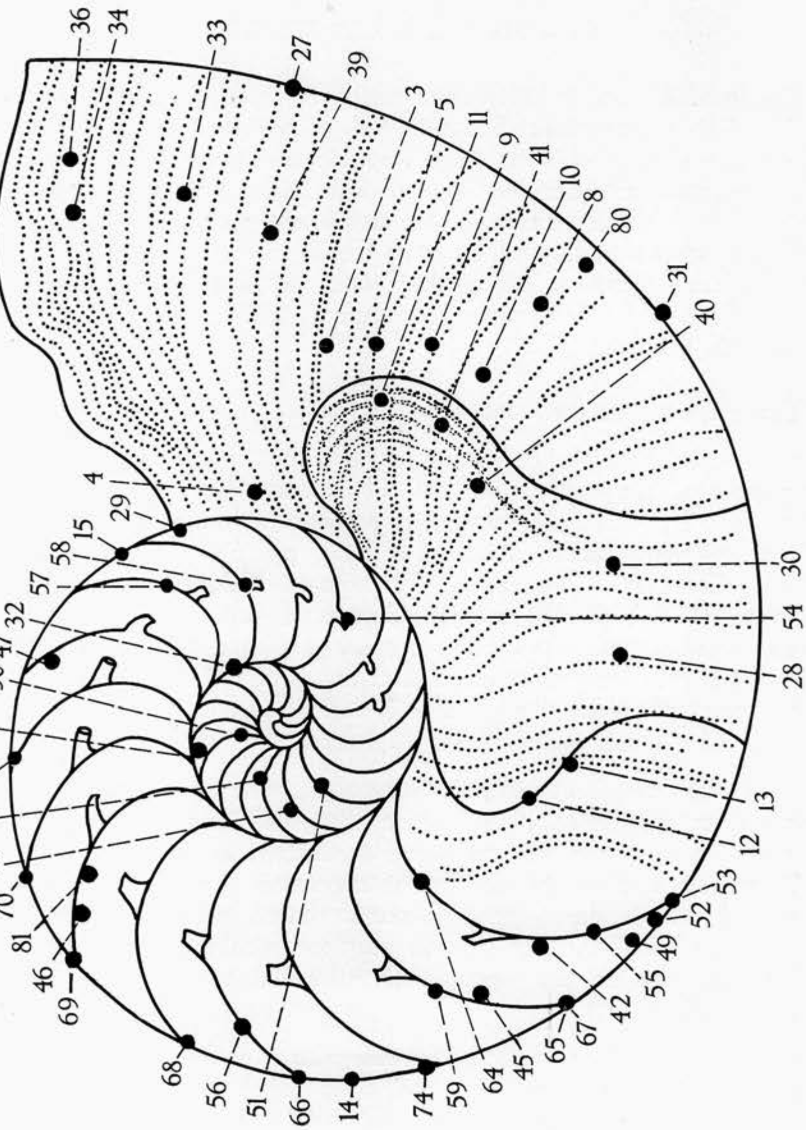
b) Membranes from the posterior convex side of the septa, membraneous discs interposed between the shell wall and the shell muscles, prepared in the same way as above or thinned by teasing.

Drops of suspensions of the disintegrated organic materials were deposited on standard copper screens coated with films of formvar (solutions of 0.07-0.1 per cent in ethylene dichloride) and of carbon. After drying in air, the preparations were shadow cast with palladium (angles : 15 to 27°).

c) Positive carbon replicas (double stage method, BRADLEY, 1954, 1955, 1960), shadow cast with palladium (angle : 15 to 27°) prepared before and after etching, of the outer and of the inner surfaces of the shell wall, of the convex and of the concave sides of the septa, of surfaces of fracture and of surfaces of polished and etched transverse sections of the shell wall and of the septa.

About 350 different preparations were examined with a R.C.A. E.M.U.-C electron microscope and with an Elmiskop 1. 1800 micrographs were recorded with the R. C. A.

(1) Generator S. C. A. M., type B, associated with a projector type L. Frequency : 960 Kcy/sec.; 90/100 Volts, 45-50 m A. Intensity : 14-20 W/sec. cm².



Textfig. 1. — *Nautilus pompilius* LAMARCK. Median longitudinal section of the shell. The black circles indicate the location of some regions recorded photographically and shown in the plates.

III. — OBSERVATIONS.

The location of the shell regions from which representative micrographs are recorded in the plates is indicated in textfig. 1.

1. The Shell Wall.

On the variously weathered outer and inner surfaces, the outlines of the crystals were generally blurred. In the outer regions of the umbilical callus and of the black deposits, colonies of diatoms were anchored in the anfractuosities. Before preparation of the replicas, these surfaces were cleaned by weak etching and successive replicas were used.

a) Outer surfaces.

The following types of structures were detected on these surfaces, including those of the flame-like, brown orange streaks, of the black deposits, and of the umbilical region :

1. Lenticular bodies, 150-200 millimicrons in diameter, generally clustered in considerable numbers (figs 2 and 7) without preferential orientation, and especially numerous along the shell aperture.

2. Dome-shaped mounds of various sizes, 200 millimicrons to 4 microns in diameter (figs 1 and 6). These mounds are composed of flat discs stacked upon one another like pancakes. The blurred hexagonal outlines of these discs appear as folded white fringes around the slopes. These mounds result from successive concentric overgrowth of crystals with a diameter decreasing towards the top of the mounds. The early stages of formation of these structures consist of hexagonal or rounded crystals with a bulging upper surface, on to which small tabular crystals are lying (fig. 5).

On the surface of the brown orange streaks, white ribbons, arranged in networks, and granules appear scattered between the mounds.

Extremely small granules, 3 millimicrons in average diameter, were observed in the anfractuosities of the surfaces of the black deposits.

In the milk-white, roughly triangular and lustreless surface of the umbilical plug, covered with small hemispherical elevations, 100-140 microns in diameter, the extremities of underlying elongated crystals which characterize the porcellaneous substance (see below) emerge at the surface.

On the surface of the iridescent nacreous crescent-shaped region which surrounds and overlaps the porcellaneous substance of the umbilical callus and a portion of the black deposits, mosaics of tabular crystals are disposed in a flagging, as usually on the surfaces of mother-of-pearl parallel to the nacreous stratification.

b) Inner surfaces.

On the inner surfaces of the living chamber, formation of new nacreous substance by crystal growth takes place, as in other shells, not only along the extending free edge of the lamellae or growth lines (Wachstumsmaserung, SCHMIDT, 1923) but also simultaneously within successive still incomplete superimposed lamellae.

Microcrystals at different stages of their development, solitary or disposed in clusters, were found on the surfaces near the axis of coiling of the shell (fig. 4) and outside the adoral edge of the muscle scars (fig. 10).

Most of the larger crystals found on the surfaces are rounded tabular elements embedded in part in nacreous conchiolin, or symmetrical or slightly asymmetrical hexagones.

The hexagones are weakly developed along their c-axis, disposed at right angle to the nacreous stratification. Development of the planes (001) and (010) (figs 3, 8 and 9) results in tabular shape and elongation of the crystals along their a-axis, which is predominantly at right angle to the growth lines.

Parallel orientation (fig. 8), aggregation of parallel grown crystals (fig. 9), with junction along the (110) or the (010) plane of the crystals, oriented overgrowth of parallel elongated seeds and of larger crystals, generally along the a-axis of the basal crystals (fig. 3) were recorded in groups of neighbouring crystals but not in others.

In the region of the living chamber posterior to the adapical edge of the muscle scars and in the whole phragmocone, the mural parts of the septa, which constitute the lateral surfaces of the camerae, overlap and conceal the inner surfaces of the shell wall.

In these regions, the surfaces examined with the electron microscope present the particularities of structure of the concave septal surfaces and will be described in a next section.

Area of insertion of the shell muscles.

In the horseshoe-shaped region of insertion of the shell muscles and of the annulus, in the living chamber, an organic substance is frequently preserved in the dried shells in the form of a rigid, semi-transparent, membraneous disc, more or less adhering to the inner nacreous surface of the shell wall.

In the living animal, this membrane is sandwiched between the epithelial layer, portion of the mantle, which lines the shell muscles, and the inner shell layer.

The replicas of the surface of the membraneous disc facing the muscle and those of the underlying shell wall show scattered bundles, variously oriented, of parallel, finely granular or fibrillar strands, separated by sharp ridges (not shown). These strands are the imprints of the microfibrillar systems which compose the membraneous disc (see below).

Numerous lenticular microcrystals (not shown), 10 to 100 millimicrons in diameter, are scattered or clustered at random on these strands.

The inner shell surface differs greatly in its appearance on either sides of the bulging ridge marking the demarcation between the adapical and adoral edges of the muscle insertions and the free inner surface of the living chamber. The latter shows the structures described above, parallel growth, concentric overgrowth and aggregation of tabular crystals. Overgrowth of tabular crystals seems to be important along the boundary and results sometimes in constitution of mound-shaped piles of crystals.

In the area of muscle attachment, the surfaces underlying the membraneous disc are covered in numerous areas with swarming small lenticular bodies, similar in their shape to those scattered over the mural surface of the membraneous disc (figs 12 and 13).

Estimation of the number of microcrystals per square mm of surface of the membraneous disc and of the shell wall in the region of muscle insertion, obtained from counts on enlarged prints, furnished the following figures : inner nacreous surface of the shell, adoral ridge of the area of insertion of the shell muscles : 2 millions; adapical ridge (4 different areas) : 41, 44, 68 and 126 millions respectively; inner nacreous surface of the shell underlying the membraneous disc (2 different areas) : 37 and 53 millions respectively; surface of the membraneous disc in contact with the muscle and with the palleal epithelium (2 areas) : 13 and 28 millions respectively.

In other fields of the areas of muscle insertion, bundles of sturdy spindle-shaped girders (fig. 11) protrude above the background in various orientations. These bundles are groups of columnar crystals from the special nacreous layer (helle Schicht or hypostrakum) which underlies the muscle insertions.

Fig. 11 illustrates the disturbance in the growth orientation of these structures, induced probably under the influence of the muscle traction (see discussion).

c) Inner architecture.

The shell wall of the recent *Nautilus* consists of two aragonitic layers, a milk-white, outer porcellaneous layer and an inner nacreous layer (VALENCIENNES, 1841; BLAKE, 1882; APPELLÖF, 1893; SCHMIDT, 1924; BØGGILD, 1930).

Outer porcellaneous layer.

Observed with the electron microscope, the characteristic mineral structures of the porcellaneous substance are variously shaped crystals appearing in the form of elongated sharp-edged tablets, blades or bars (figs 15, 17, 18, 19, 21-24, 27), of bulging discs or of rounded lenticular corpuscles (figs 25, 26). When seen along their edges, in cross or oblique sections, the same elements resemble girders, shafts, beams, rods, needles or spindles.

Arrangement of these crystals differs in the outermost and in the innermost parts of the outer layer.

On surfaces of polished and etched transverse sections of the outermost and middle parts of the outer layer (figs 14, 17, 18), the parallel imbricated elongated crystals are generally disposed in groups. In these groups, the individual crystals are separated from one another by thin layers of substance visible on the replicas as white ribbons or shreds of membranes (2).

In some of these groups, the crystals are disposed radially in corpuscles or they diverge in a feather-like arrangement from central elongated stems (figs 17 and 18). Parallel imbricated crystals form also bundles, in which the crystals run at very different angles with those of the adjacent bundles (fig. 19). As shown in fig. 14 (right) and in fig. 17, several neighbouring bundles of elongated crystals appear involved obliquely, tangentially or at right angle to the plane of polishing.

Several groups or bundles may compose large corpuscles, several microns in diameter (fig. 17).

On surfaces of polished and etched cross sections of the inner part of the outer layer, contiguous to the inner nacreous layer, the elongated crystals are generally disposed in palisades, at right angle to the nacreous stratification (fig. 15). Groups of such elongated crystals, notched into the laminary nacreous structure, interrupt locally the regularity of the nacreous lamellar stratification (fig. 14, left).

In the brown orange coloured regions of the outer layer corresponding to the flame-like streaks, granular strands of unknown nature, scattered between the elongated crystals of the porcellaneous substance, were detected on the surfaces of the polished and etched cross sections of these areas.

Inner nacreous layer.

This layer shows the brick wall (EHRENBAUM, 1885; W. J. SCHMIDT, 1924) configuration of mother-of-pearl : superimposed mineral lamellae, 150-200 millimicrons in average thickness, composed of tabular crystals

(2) A part of these shreds are artifacts and represent moulds of microcracks developed in the etched mineral surfaces between the crystals (see discussion, GRÉGOIRE, 1961, p. 17).

These moulds, stripped from the surfaces with the first, plastic replica, are metallized during carbon evaporation on this replica and the subsequent shadow casting with palladium of the positive carbon replica.

A discrimination on the micrographs between true organic membranes and these replicas of cracks is frequently difficult and sometimes impossible. Indirect evidence of the presence of organic material sandwiched between the mineral elements is provided by detection in thoroughly decalcified preparations of organic residues with a structure identical to that of the membranes appearing in the replicas (see below).

of aragonite aligned side by side, alternate with organic sheets. The lamellae, parallel to the inner surfaces of the shell wall in the relatively levelled regions of the living chamber (figs 31 and 31a), are less regularly disposed (figs 29 and 32) in the regions in which the shell is strongly curved, especially in the neighbourhood of the axis of coiling.

In contrast with the disposition of the crystals of aragonite in the nacreous lamellae of many other shells, the margins of the aragonite crystals in mother-of-pearl of *Nautilus* coincide frequently, but not consistently, in the successive superimposed lamellae. In transverse sections of the layer, the crystals appear stacked in columns (figs. 31 and 31 a).

Periodic alterations in the regularity of the nacreous stratification were observed in several regions of the shell wall. Fig. 27 shows, in a transverse polished and etched section, groups consisting of several thin successive lamellae alternating with single lamellae with different thickness and orientation of their crystals (see also fig. 31). Fig. 27 illustrates also the modifications in the configuration of mother-of-pearl at its boundary with the porcellaneous substance. In this region, the lamellar nacreous stratification becomes irregular. Wedge-shaped horizontal crystals of aragonite are scattered among porcellaneous elements oriented at right angle to the nacreous stratification (upper left portion of fig 27). Intrication of irregularly shaped crystals belonging to both layers does not always permit to distinguish the actual boundaries of these layers.

Fig. 30 shows in the region of insertion of the shell muscles the elongated crystals of the helle Schicht or hypostrakum which characterize the structure of the innermost mother-of-,pearl in that region.

A former helle Schicht embedded in nacreous substance grown upon it after the muscle moved forward in the shell appears in transverse section as a thick lamella with columnar crystals interposed between thinner nacreous lamellae of the regular stratification (fig. 28).

Umbilical callus.

The milk-white porcellaneous substance which composes the umbilical callus has been studied on surfaces of polished and etched transverse sections of the shell.

The same elements which characterize the porcellaneous layer of the shell wall are found in the callus. Different aspects of the association of these porcellaneous crystals in bundles, plates and pillars are shown in figs 16, 19-21, 25 and 26.

In fig. 16, a group of elongated elements diverge from a central stem in a feather-like disposition. In fig. 19, a group of parallel elongated crystals is notched like a wedge into neighbouring groups with thoroughly different orientation of their crystals.

In fig. 21, bundles in the form of sturdy pillars are composed of parallel imbricated elongated tablets of irregular shapes, and of lenticular bodies attached to the elongated structures. Similar lenticular bulging bodies disposed without distinct orientation are shown in fig. 25. Imbrication of elongated tablets or rows of lenticular bodies appears in fig. 26. In other fields (not shown), parallel crystals are disposed in stratified concentric arch-shaped arrangements.

In preparations of fractured callus near the axis of coiling of the shell, the surface of fracture shown in fig. 20 is subdivided into large spindle-shaped fields composed of mosaics of roughly square bulging structures superimposed in diverging columns and separated by membraneous substance. These stacked square structures are possibly cross sections of elongated crystals grouped radially in bundles or in plates.

In several peripheral portions of the umbilical callus, the porcellaneous substance is directly juxtaposed to the nacreous substance of the septa and of the crescent-shaped layer which overlaps a part of its outer surface in the umbilical region.

In some of these areas, extremely thin flexuous or wedge-shaped fringes of porcellaneous substance, visible at low magnification on polished cross sections of the shell, form deep indentations in the nacreous substance, shown in figs 22, 23 and 24.

The porcellaneous fringes are composed of the characteristic elongated tablets (fig. 23) appearing as rods, needles, spindles, beams, girders in transverse or oblique sections.

These crystals, disposed at right angle to the nacreous stratification (figs 23 and 24) are aligned more or less regularly in loose (fig. 23) or imbricated in dense (fig. 24) palisades.

The arrangement in rows and the shape of the crystals of aragonite in the nacreous lamellae adjacent to the porcellaneous substance of the fringes are altered. In fig. 22, an irregularly shaped tabular crystal belonging to a nacreous lamella, located at the boundary of a fringe, seems to be soldered without any visible demarcation with an elongated club-shaped expansion oriented at right angle to it and to the nacreous stratification. The development of the porcellaneous material seems to have driven back a group of nacreous lamellae (upper left side of the figure).

In fig. 24, alteration in another nacreous crystal of aragonite (upper side of the figure, see legend) consists of increase in thickness along its c-axis, and development of two rod-like expansions disposed obliquely to the crystal body. These expansions disturb the regularity of the next nacreous lamella. Along the boundary of the fringe (above the black spot in the figure), irregularly shaped crystals are interposed between the last nacreous lamella and the elongated crystals of the porcellaneous substance.

d) Structure of the organic components.

The organic remnants of decalcified shell fragments and of dust from filed outer and inner layers were examined without further treatment or after mechanical thinning by teasing and by ultrasonic disintegration.

Organic components of the outer layer and of the umbilical callus.

After decalcification of the outer shell layer, the organic residues appear as semi-rigid shreds. These fragments are opaque to the electron beam and are resistant to ultrasonic waves. Their suspensions remain transparent and do not become iridescent.

Observed on their thinnest edges, the disintegrated shreds are composed of dense microfibrillar layers arranged in feltings or in meshworks, in which the fibrils, 4 to 6 millimicrons in diameter, solitary or associated in bundles, are embedded in thin amorphous veils (figs 33, 34 and 36).

In contrast with the porcellaneous material of the shell wall, the organic components of the decalcified porcellaneous substance of the umbilical callus were easily disintegrated into identical fibrils by mere shaking of their suspensions.

Decalcified dust from filed substance of the flame-like coloured streaks reveals orange coloured shreds. This material, dissociated by ultrasonic waves and sedimented on formvar films, is composed of rounded bodies of various sizes. These bodies are aggregates of small particles, scattered or aligned in contorted strands (figs 35 and 37). Fibrils, 4 to 6 millimicrons in diameter, intermingled with the groups of particles, belong to the components of the outer layer of the shell wall.

The black deposits, collected by peeling off the outer surface of the shell and immersed in decalcifiers, leave dark brown particles in aqueous suspensions, in which a pink hue develops during ultrasonic disintegration. This material appears in the electron microscope as homogeneous particles, 3 millimicrons in diameter (fig. 38).

Organic components of the inner layer.

As shown previously in *Nautilus macromphalus,* the soft iridescent organic membranes, freed by decalcification of the inner nacreous layer of the shell wall, are rapidly cleaved and broken by ultrasonic waves into submicroscopic fragments. Their aqueous suspensions become strongly glistening with bluish hues already after an exposure of a few seconds.

These fragments appear in the electron microscope as lace-like reticulated sheets.

Prepared by the same procedure, the organic sheets of *Nautilus pompilius* resemble closely in their texture those of *Nautilus macromphalus.* Fig. 39 shows two fragments of organic leaflets, portions of the conchiolin membrane on which tabular crystals of aragonite were originally superimposed. The lace-like structure consists of sturdy trabeculae, 30 to 40 millimicrons in diameter, which separate rounded or elongated openings of irregular outlines. The trabeculae, sprinkled with bulging hemispherical tuberosities of various sizes (from 4 millimicrons to 26 millimicrons in diameter) appear as knobby cords resembling frequently the rhizomes of the garden iris (GRÉGOIRE, 1957, 1958).

The stratified membraneous disc which overlies the inner layer of the shell wall in the region of the muscle scars, is cleaved by teasing after decalcification into thinner glassy and rigid tablets, opaque to the electron beam. Examination of the thinnest edges of these teased fragments reveals microfibrils, 3 to 4 millimicrons in diameter. These microfibrils, which appear stretched in fig. 40, form extremely dense feltings.

The membranes, cleaved into thin plate-like shreds, are still extremely resistant to ultrasonic waves. Their aqueous suspensions remain clear or become slightly foggy even after protracted exposures. Fig. 41 shows in a dissociated shred, sets of loosely sedimented microfibrils, isolated or grouped into fibers. Individual fibrils, 5 millimicrons in diameter, seem to be sometimes composed of aligned rounded particles. However, evidence of nodulation in these fibrils is ambiguous.

The Septa.

a) Adapical, convex surfaces.

It has long been reported (WOODWARD, 1851; BARRANDE, 1857; HYATT, 1872, APPELLÖF, 1893) that the inner surfaces of the camerae in dried *Nautilus* shells are coated with a thin, brownish-yellowish, lustreless substance. This substance covers uniformly the convex sides of the septa and has generally disappeared, but in scattered areas as a discontinuous formation, in *Nautilus umbilicatus* (APPELLÖF, 1893), from the other (mural and concave) surfaces of the camerae.

In various sites of the convex sides, especially in the freshly opened small adapical camerae, this coating appears spontaneously detached from the septal surfaces in the form of transparent crumpled membranes, sprinkled with mineral corpuscles.

In the areas in which the brown layer adheres firmly to the underlying nacreous layer, it is consistently removed from the convex side of the septa with the plastic films used as negative replicas. In these areas, the bright iridescent underlying nacreous surfaces are then exposed.

In dried shells, the brown lustreless convex surface of the septa is characterized on positive replicas examined with the electron microscope by the presence of scattered pyramidal or conical mounds, some one micron in diameter, with steep terraced slopes and blunted, sometimes faintly hexagonal (010) (110) outlines.

These mounds (fig. 42) erected over the surfaces, consist of several concentrically superimposed irregular flat discs or rounded crystals. The size of these crystals decreases towards the top of the mounds.

The background on which the mounds are lying is smooth or finely granular. It is covered, especially in the early camerae, with debris of an organic microfibrillar layer (diameter of the fibrils : 5-6 millimicrons) which surround the mounds (figs 43 and 44) and which are the remains of the membrane coating the posterior side of the septa.

The faint limits of polygonal crystals belonging to the underlying nacreous layer are sometimes visible between the mounds.

b) Adoral, concave surfaces.

Except for scattered areas coated with brownish remnants of the organic substance mentioned above, the concave sides of the septa in freshly opened camerae of dried shells appear brightly iridescent with a greenish hue. Faint traces of various growth patterns (parallel, spiral, irregular and concentric : W. J. SCHMIDT, 1923-1924; WADA, 1961, in Pelecypods) were visible in some areas of the cameral surfaces, especially in their mural portions.

The concave sides of the septa may be subdivided into a free and a mural parts (FOERSTE and TEICHERT, 1930; TEICHERT, 1933).

On the surface of the free parts, large flat crystals with their tabular (001) plane smooth or overgrown with crystals of various sizes, are scattered or grouped on the background of the last formed, still incomplete, nacreous lamella (figs 45 and 46).

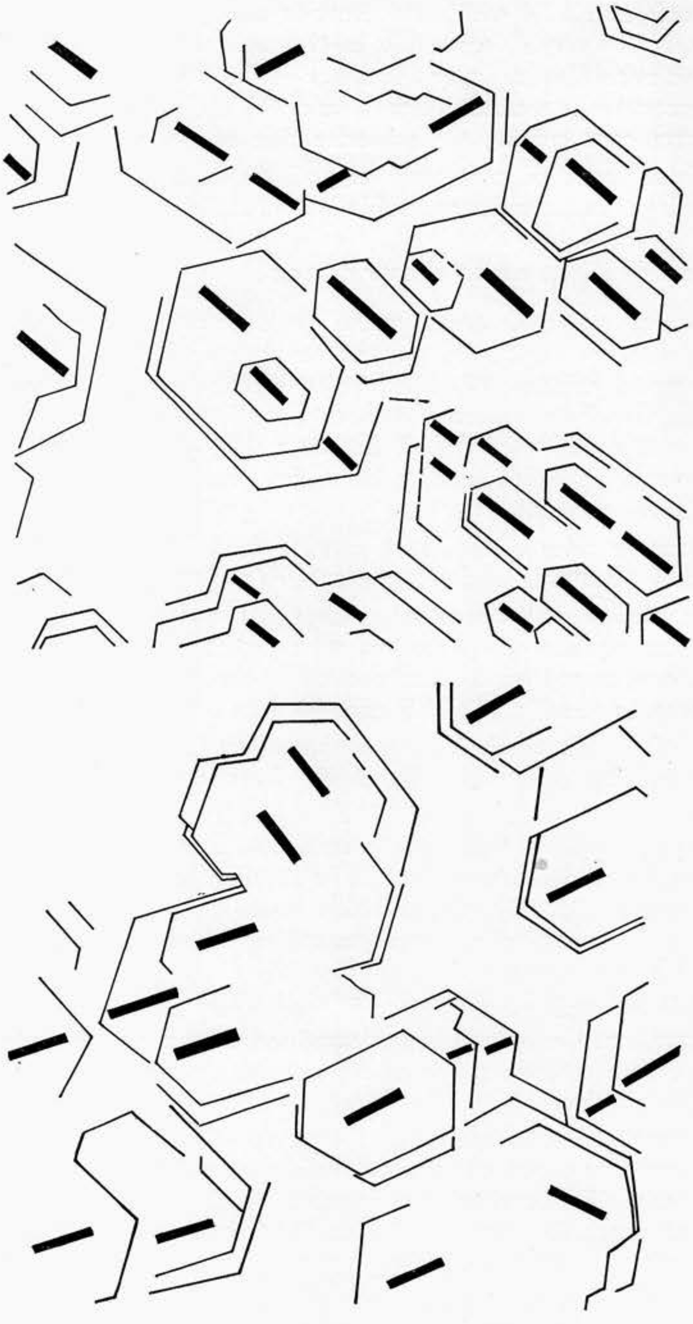
Debris of reticulated sheets with a dense texture surround and overlap the crystals (fig. 46), especially in the freshly opened small adapical camerae.

The crystals, with a predominant hexagonal shape (001) (010) (110), are disposed without any definite or with slightly diverging orientation in some areas (fig. 46). Other fields (textfigs 2 and 3, fig 45) are characterized by parallel oriented growth of the crystals, parallel overgrowth, and aggregation.

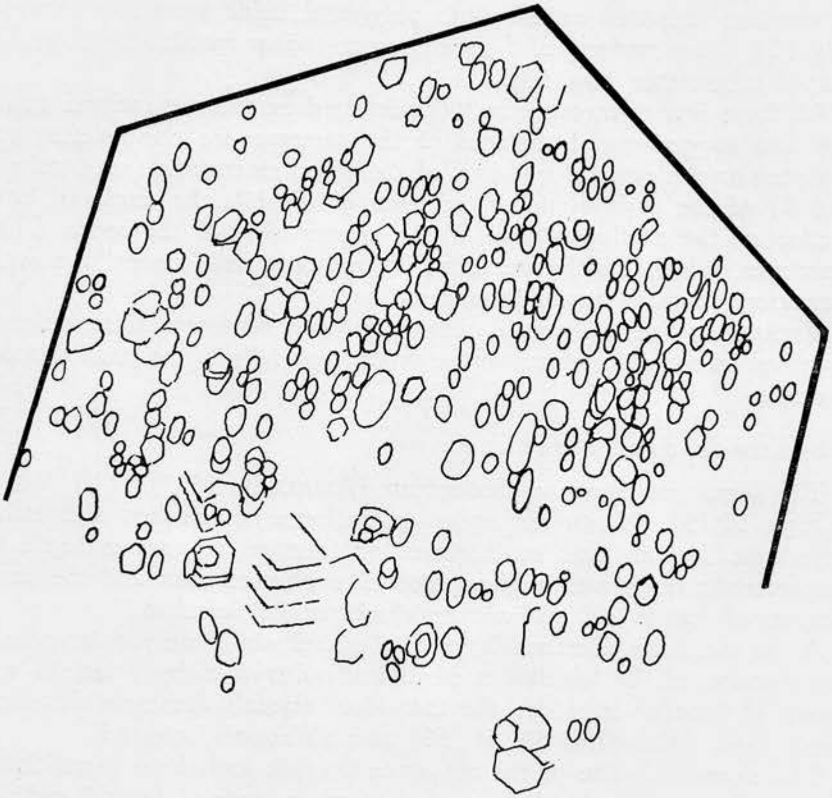
In the lower right part of fig. 45, four layers of superimposed crystals indicate that the four youngest stratified nacreous lamellae were still incomplete on the concave side of the penultimate septum, at the time of death of the animal.

Well preserved reticulated sheets of conchiolin were found collapsed on to the concave septal surfaces of freshly opened camerae. In the sheet shown in fig. 47, the slender trabeculae which characterize the septal pattern of conchiolin are parallel to the a-axis of the neighbouring crystals (see discussion).

Fig. 83 shows a reticulated sheet of conchiolin underlying the outlines of a large hexagonal crystal of the concave surface of the last but five septum. In this preparation, a definite orientation of the trabeculae along the a-axis of the crystal (directed from bottom to top of the figure) is recognizable.



Textfig. 2. — See fig. 45. *Nautilus pompilius* LAMARCK. Two representative fields of the concave adoral surface of the penultimate septum. The outlines of hexagonal crystals and the direction of their a-axis (thick lines) are shown. The crystals exhibit parallel growth and overgrowth, aggregation predominantly along the (010) plane. Note the divergent direction of the a-axes in closely adjacent groups of crystals.



Textfig. 3. — *Nautilus pompilius* LAMARCK. Concave adoral surface (unetched) of the penultimate septum.

The drawing shows the outlines of a large hexagonal crystal with substantial parallel overgrowth on its (001) plane and along its a-axis (slightly oblique from top right to bottom left) of elongated and hexagonal microcrystals.

In their bright iridescent adapical portion, near the septal curvature, the surfaces of the mural parts of the septa do not differ in their appearance from those of the adjacent concave free portion.

More adorally, heterogeneous structures appear on the mural surfaces of the septa (figs 48, 49, 52, 53). The large tabular hexagonal crystals are absent. Rounded mulberry-like eminences, and irregularly conical mounds, disposed without orientation, protrude on anfractuosities of the background. As in similar structures described above on the outer shell surfaces and on the convex sides of the septa, these eminences and mounds seem to consist of superimposed layers of flat crystals or of lenticular bodies, either solitary or aggregated in each layer (multiple overgrowth) (fig. 48).

Still more adorally, bundles variously oriented made up of parallel elongated girder-shaped crystals (fig. 49) emerge at the surfaces. Groups of elements disposed radially into polygonal fields were also recorded (fig. 52). Other surfaces of the same region appear sprinkled with pebble-shaped tuberosities (fig. 53).

All these heterogeneous structures detected on the most adoral, lustreless and rugged mural surfaces of the camerae are components, outcropping on the cameral surfaces, of the mural extensions (see textfigs 4 and 5) of the organo-mineral complex which fills the angle of intersection of the shell wall and of the convex side of the septa. These structures, which will be described below, coat and conceal the septal formations in their most adoral mural parts.

Various degrees of crystal dissolution and of recrystallization were observed on several surfaces of the septa, especially in the small adapical camerae.

c) Inner architecture.

The septa are nacreous throughout (APPELLÖF, 1893).

Figs. 50, 51, 55 and 56 show on surfaces of polished and etched transverse sections and on surfaces of fracture of various septa the characteristic brick wall configuration of mother-of-pearl and the stratification of 150 to 200 millimicrons thick parallel lamellae.

As in the inner nacreous layer of the shell wall, the regular parallel stratification of the lamellae is periodically disturbed by a lamella or a group of lamellae in which the individual crystals are more developed along their c-axis (figs 50, 51, 55) and differently oriented.

The shape and size of the aragonite crystals and their disposition in the lamellae vary in the different septa (see legends of figs 50 and 55).

In the thin adapical septa (seen in transverse section in fig. 50), the lamellae are frequently characterized by an irregular alignment of the crystals and by predominance of small lenticular crystal forms. These disposition and shape of the crystals suggest a rapid superimposition of successive incomplete lamellae. In the individual lamellae already involved in the stratification, and overlapped by new nacreous layers, unoriented crystal growth continues probably in the gaps left between the existing crystals.

On the other hand, large crystals of aragonite such as those shown in figure 55, and regular stratification (fig. 56) in broad areas, observed in transverse sections of the adoral septa, suggest that the constitution of these septa, especially the ultimate one, took place at a slower pace than that of the early adapical septa.

Figs. 54 and 58 show two representative structures of the inner calcareous ring of the siphonal funnel which coats inwards the septal mother-of-pearl : parallel elongated crystals grouped in bundles variously oriented (fig. 54) and, more inwardly, sturdy elongated girders in a brush-like arrangement which line the funnel opening (fig. 58). The latter structures are the spicules described with the conventional microscope (BROOKS, 1882; APPELLÖF, 1893 : Pl. XI, figs 2 and 4; MUTVEI (1956).

d) Structure of the organic components.

Nacreous conchiolin.

The organic material freed by decalcification of the septal mother-of-pearl shows the texture of the nacreous conchiolin of the shell wall. However, the fabric of the septal reticulated sheets is generally denser (compare figs 57 and 59 with fig. 39 : same magnification). The trabeculae, about 18 to 35 millimicrons in diameter, on which hemispherical protuberances, predominantly of small size (about 5 to 10 millimicrons in diameter), are similarly scattered, are more slender, the openings smaller and rounder.

An identical texture characterizes also the septal conchiolin sheets immediately underlying the posterior membrane, on the convex side of the septa.

Posterior membrane.

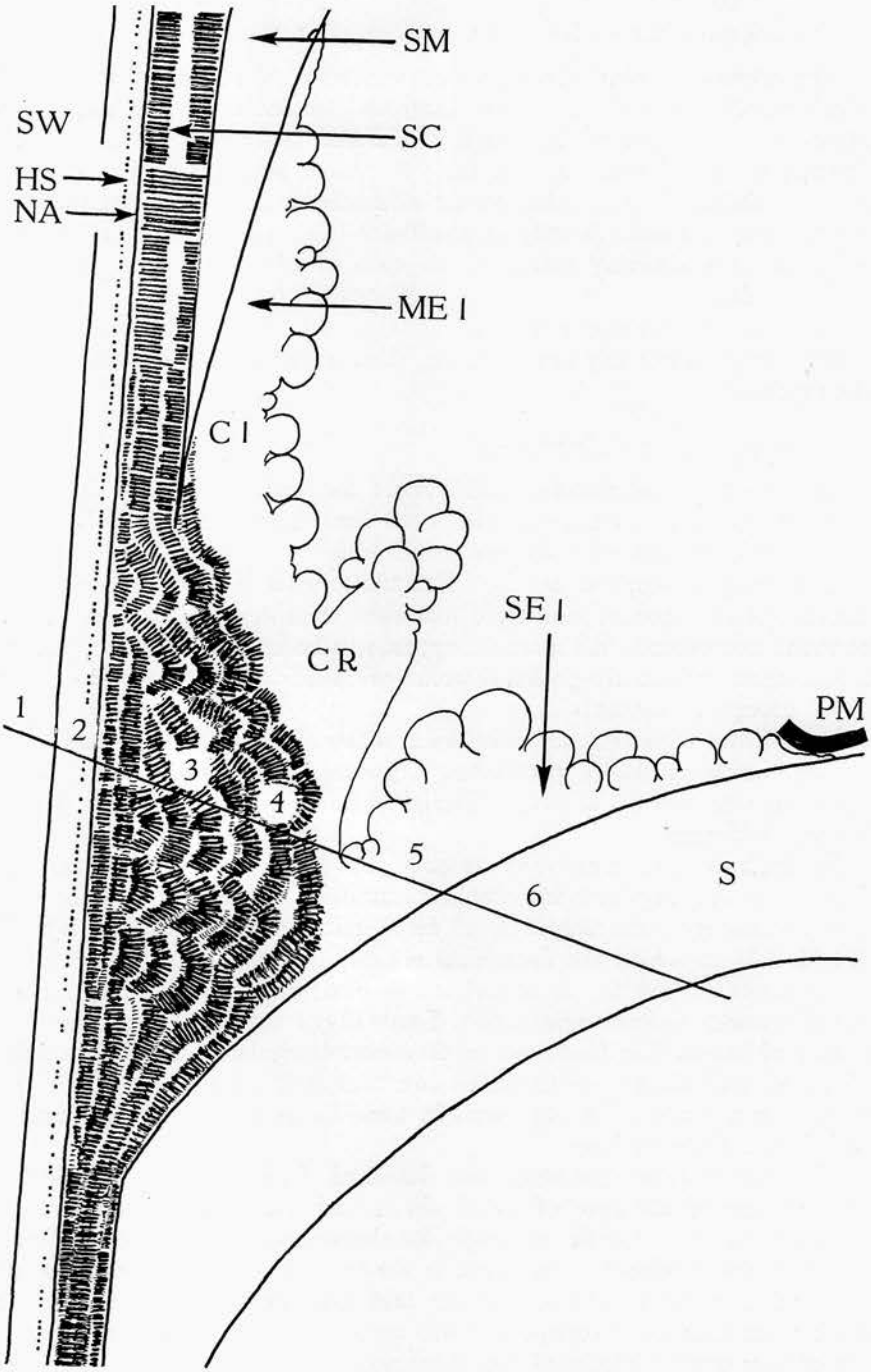
The posterior membrane, which coats the convex side of the septa, thoroughly differs in its structure from the immediately underlying iridescent membranes of nacreous conchiolin.

The sample supplied by Dr. Teichert used in the present study consists of transparent semi-rigid lustreless membranes. Under the phase contrast microscope, this material appears to be sprinkled with numerous bright spots, which are probably areas of calcification composed of scattered groups of crystals.

In contrast with the soft conchiolin sheets, the posterior membrane is hardly disintegrated by protracted exposure to ultrasonic waves : the aqueous suspensions of this material remain transparent and do not become iridescent.

Portions of the membrane thinned by teasing with tweezers and fragments resulting from ultrasonic dissociation, examined with the electron microscope, are composed of dense microfibrillar feltings (figs 60, 61, 62, 63) in which the individual microfibrils, 4 to 8 millimicrons and up in diameter, solitary or associated in bundles forming fibers, are disposed without definite orientation. Some fibrils seem to be composed of chains of beads, 3 millimicrons in diameter. Irregularly rounded nodules, 25 to 40 millimicrons in diameter, are scattered among the fibrils, and sometimes are aligned along them. In some fields, the microfibrils anchor radially to these nodules.

The membranes spontaneously detached from the convex side in freshly opened camerae of dried shells had the same texture. In the adoral, youngest camerae, in which the altered membranes adhered firmly to the convex surfaces of the septa in the form of a brownish coating, the same material collected by stripping and examined after decalcification, did not contain but occasional fibrils and consisted in most samples of amorphous opaque blocks of substance mixed with typical lace-like sheets of nacreous conchiolin trom the underlying layer.


SM
SW
SC
HS
NA
ME I
C I
SE I
CR
1
2
3
4
5
6
PM
S

The connections between the posterior membrane of the convex side of the septa and the underlying reticulated sheets of nacreous conchiolin were studied on surfaces of polished and etched cross sections of the septa.

Fig. 64 shows (above) variously folded fibers of the posterior membrane and below the nacreous conchiolin consisting of parallel interlamellar shreds united by intercrystallinic bridges.

Textfig. 4. — Polished transverse section of the *Nautilus* shell, showing the location of the sutural cements and infillings at the angle of intersection of the shell wall and of a septum.

From left to right:

a) the innermost nacreous substance of the shell wall (S W, 1);

b) a former helle Schicht (H S, 2) or nacreous substance modified in its structure (columnar instead of tabular crystals) in the regions of previous insertion of the shell muscles, and covered with a thin layer of mother-of-pearl (N A) grown over it after the forward adoral motion of these muscles on the inner shell surface. This nacreous layer shows disturbances in its stratification at the boundary of the next layer;

c) the sutural cements and infillings. These heterogeneous substances include the linear cement (S C) interposed between the shell wall and the wedge-shaped extremity extending adorally of the mural part of a septum (S M), and the diverging expansions of this substance at the angle of intersection (3 and 4).

The columns of parallel dashes, festooned in the area of expansion of the cements, indicate the location of the milk-white layers or palisades, made up of elongated imbricated tablets appearing as girders, beams, rods, needles or spindles when viewed on their edges.

The layers of palisades alternate at irregular intervals with variable numbers of brownish layers of organic substance (3: in white on the drawing).

The sutural cements are covered towards the camerae with yellowish infillings composed of calcareous concretions (M E I, C I, C R, 5 and S E I). These concretions extend in the form of terraces (S E I) over the posterior convex side of the septum (S, free part) and over the mural portion of the preceding adapical septum (M E I) where they conceal these surfaces over variable distances.

Between the septal and mural extensions of the calcareous concretions, a crest (C R) of the same substance protrudes into the cameral cavities.

All the surfaces of the calcareous concretions are sprinkled with grape-shaped tuberosities and assume a mulberry-like or mammillated appearance;

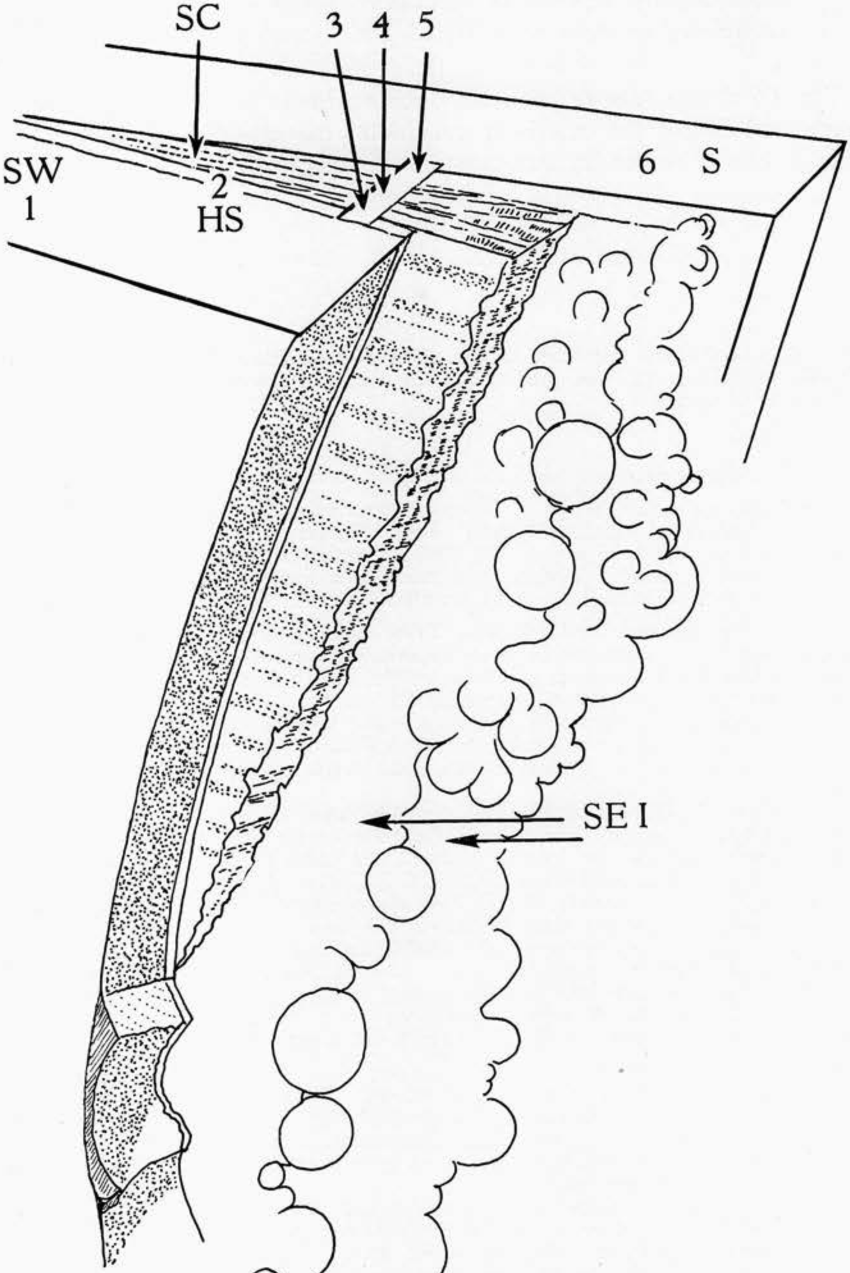
d) in the camerae of the middle and adapical parts of the phragmocome of dried shells, fragments of the septal posterior membrane (P M) overlap the lowest terraces of the calcareous concretions and intermingle with them.

This drawing has been combined from observations of about twenty different areas. The disposition of the various layers varies greatly in the different angles of intersection of a same phragmocone.

In this drawing, the wedge-like extremity of the septum shown on the upper side of the figure has been shortened and appears thicker than it is actually.

In the electron microscope, the ends of the mural parts of the septa appear in the sections as a few lamellae of nacreous substance sandwiched between the components of the sutural infillings, the cements on one side and the calcareous concretions on the other side. These lamellae seem to disappear at some distance of the next adoral septum.

The oblique line indicates the location of the region drawn in textfig. 6 and the figures disposed along this line correspond to those of the latter drawing.


SC
3
4
5
SW
1
2
HS
6
S
SE I

The limit between nacreous conchiolin and the posterior membrane (middle part of the figure) appears as a continuous straight line under which shreds of amorphous material are folded on to the underlying nacreous surface. These shreds are either replicas of the interspaces separating originally the septal nacreous substance from the posterior membrane, or replicas of microcracks in the embedded material developed during the etching process.

In both contingencies, the configuration of this area suggests that the two organic substances juxtaposed on the convex side of the septa, nacreous conchiolin and posterior membrane, thoroughly different in their structure, might be merely superimposed in that region without direct anatomical connection.

3) Sutural substances (cements and infillings).

Topography.

A wedge-shaped plug composed of several substances and filling the angle formed by the shell wall and the convex sides of the septa has long been described (VALENCIENNES, 1841; BLAKE, 1882; APPELLÖF, 1893; POMPECKJ, 1912; M. SCHMIDT, 1925). Little is known about the microstructure of these substances.

The sutural cements and infillings may be subdivided into three groups :

1. A substance (textfigs 4 and 5 : SC) sandwiched between the inner nacreous layer of the shell wall (textfigs 4 and 5 : SW and 1, and fig. 65), including the helle Schicht (textfigs 4 and 5 : HS and 2) and the few irregular nacreous lamellae overlapping this layer in the phragmocone (textfig. 4 : NA) on one hand, and the mural parts of the septa (textfig. 4 : SM; textfig. 5 : S, 6) on the other hand.

In polished transverse sections of the phragmocone, this cement appears with the naked eye as a milk-white linear strand interposed between the brownish adjacent nacreous portions of the shell wall and those of the septa.

Textfig. 5. — *Nautilus macromphalus* SOWERBY.

Surfaces of fracture of the shell at the angle of intersection of the shell wall and of the ultimate septum.

S W, 1 : Inner nacreous layer of the shell wall; H S, 2 : helle Schicht; S C : Sutural cement between the shell wall and the convex side of the septum (S, 6).

The rectangular area indicates the location of the layers diagrammatically drawn in textfig. 6. The septal extensions of the calcareous concretions (S E I) are represented in the diagram as forming two terraces spreading over the convex side of the septum (S, 6). Numerous grape-shaped globular excrescences are bulging on the terraces.

This cement has been called « X-substance » by APPELLÖF (1893 : Taf. XI, fig. 1 x).

2. The prolongation and the extension of the X-Substance in the angle made by the junction of the shell wall and of the convex adapical sides of the septa, where it appears in transverse sections as a triangular area (textfig. 4 and APPELLÖF, 1893, Taf. XI, fig. 1 *x'*). The apex of the triangle is directed towards the convex sides of the septa. The two other angles extend in adapical and in adoral directions into the linear cements (see 1).

In polished transverse sections of the phragmocone, the triangular area is characterized (textfig. 4 : 3, 4) by alternating white strands and darker layers, parallel to the basis of the triangle and diverging slightly towards its apex from the adapical and adoral thinner portions. The white strands themselves are crossed by an extremely thin striation.

3. Yellowish calcareous deposits, concretions or infillings, which overlap the enlarged triangular areas of the X-Substance towards the cameral cavities (textfigs 4 and 5 : 5). The demarcation between the two structures is not sharp.

This material has been described by APPELLÖF (1893) as a chitineous infilling (« Ausfüllungsmasse ») in which rounded or elongated calcareous crystals are embedded.

These infillings form ridges or crests (textfig. 4 : C R) which protrude into the cameral cavities, and extend along narrow bands over the mural surfaces (textfig. 4 : M E I) in the form of rounded elevations and globular concretions visible with the naked eye, which confer locally to the wall a mulberry-like or mammillated appearance.

In this region (see description of the septal surfaces) the cameral surfaces of these infillings, which conceal the mural parts of the septa, differ thoroughly from those of the adjacent free septal surfaces located adapically.

TABLE 1.

Variations in the distribution of the layers in the sutural cements and infillings in regions of intersection of the shell wall (left) and of the septa (right), in *Nautilus pompilius* and in *Nautilus macromphalus*.

1. Inner nacreous layer of the shell wall; 2. Helle Schicht and overlapping altered nacreous lamellae; 3. Strands of organic amorphous substance; 4. Palisades of parallel tablets; 5. Calcareous concretions or infillings; 6. Septal mother-of-pearl (see textfigs. 4 and 6). The upper rows of the table correspond to the linear cements in the shell wall. The lower rows represent the enlarged portions of the cements and of the infillings.

1 - 2 - 4 - 6.

1 - 2 - 4 - 3 - 4 - 6.

1 - 2 - 4 (fig. 74) - 3 - 6.

1 - 2 - 4 - 3 - 4 - 6.

1 - 2 - 3 - 4 - 4 - 6.

1 - 4 - 3 - 5 - 4 - 6.

1 - 2 - 4 - 3 - 4 - 6.

1 - 2 - 4 - 3 - 4 - 6.

1 - 2 - 3 - 4 - 3 - 4 - 6.

1 - 2 - 4 - 4 - 6 (wedge-shaped end of the mural part of the preceding adapical septum : Textfig. 4 : S M) - 4 - 6.

1 - 2 - 3 - 3 - 3 - 4 - 6.

1 - 2 - 4 - 4 - 3 - 3 - 6.

1 - 2 - 3 - 4 - 3 - 4 - 4 - 4 - 4 - 6.

1 - 2 - 3 - 4 - 4 - 4 - 4 - 4 - 4 - 6.

1 - 2 - 4 - 3 - 4 - 3 - 3 - 3 - 4 - 4 - 4 - 6.

1 - 2 - 4 - 3 - 3 - 4 - 3 (fig. 66) - 4 - 3 - 4 - 4 - 4 - 4 - 6.

1 - 2 - 3 - 4 (fig. 65) - 4 (fig. 68) - 5 - 3 - 3 - 3 - 3 (fig. 67) - 4 - 5 (fig. 69, fig. 70) 5 - 4 - 6.

The infillings spread also over the convex sides of the septa in the form of superimposed terraces (textfigs 4 and 5 : S E I).

Structure.

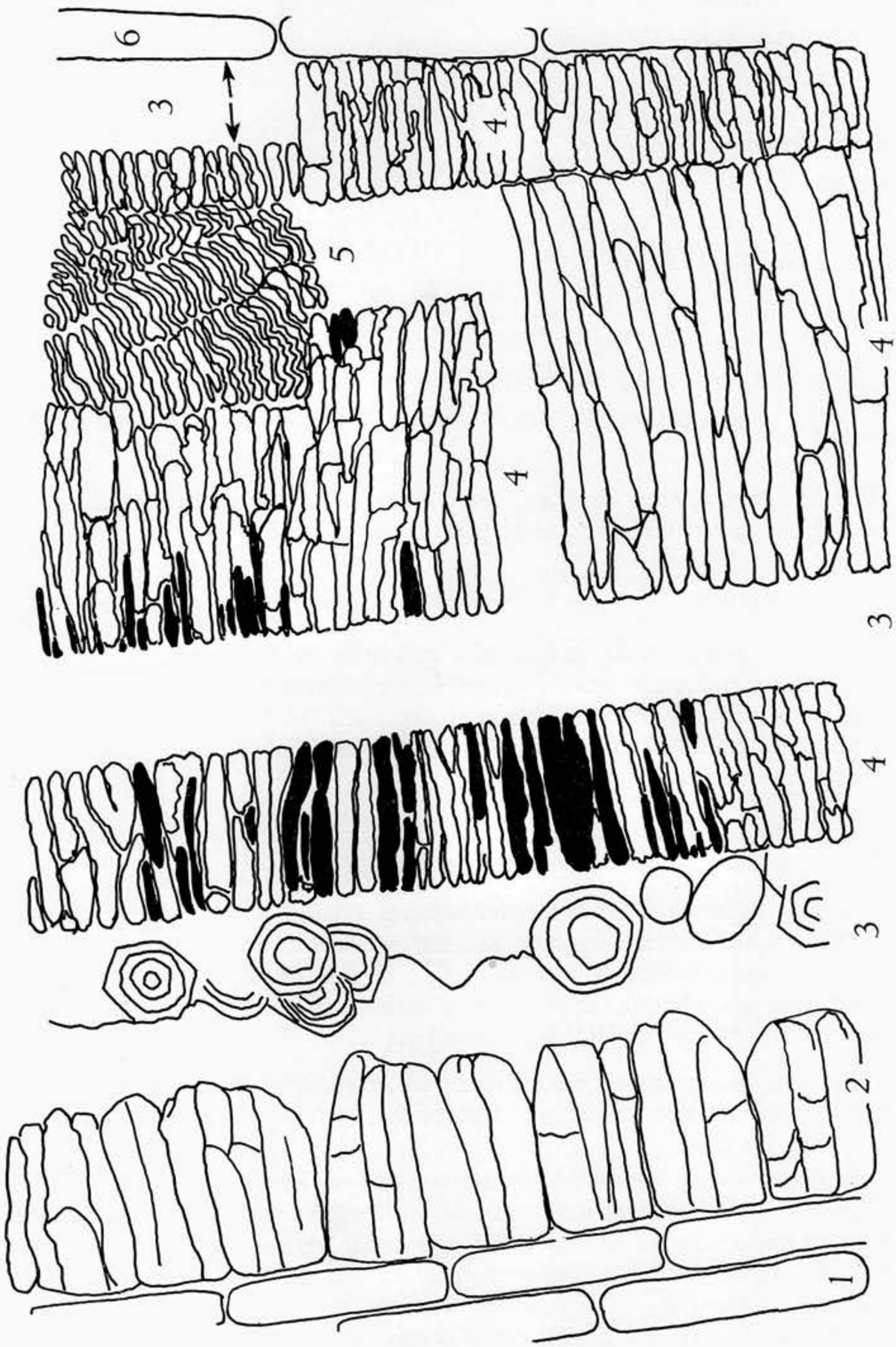
In the present investigation, the structure of the sutural substances and their distribution have been studied with the electron microscope in seventeen regions of intersection of the shell wall and of the septa on replicas of polished and etched transverse sections of the phragmocone of several shells.

The cements and infillings are composed of three kinds of microstructures, diagrammatically illustrated in textfig. 6 :

1. The milk-white cross-striated strands consist of parallel, irregularly shaped, sharp-edged elongated tablets, imbricated and piled up in rows or palisades (textfig. 4) at right angle to the length of the strands. In transverse and oblique sections, these tablets appear as needle- or spindle-shaped structures (textfig. 6 : 4 and figs 66, 68, 74).

2. The darker layers which alternate irregularly with the milk-white strands are composed of an amorphous, probably organic substance (textfig. 6 : 3).

In polished and etched transverse sections of the phragmocone, the surfaces of these layers appear concave, or convex, or they are subdivided into sublayers by smooth undulating ridges, or conversely into bulging roughly square areas by furrows crossing one another at right angle or obliquely (fig. 67). Crystals of various sizes (microcrystals, larger hexagonal or rounded elements and pyramids composed of concentrically overgrown flat hexagonal discs (textfig. 6 : in 3) embedded at random


6
3
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3
2
1

in the amorphous substance, emerge on the polished and etched surfaces of these layers. Imprints of fibrillar latticeworks were also occasionally observed on the surfaces of this amorphous substance.

3. The calcareous concretions or infillings are highly heterogeneous in structure. They include elongated tablets or blades, oriented in bundles or scattered at random, pebble-like rounded corpuscles (fig. 53), thinly stratified amorphous calcareous substance, forming whirlpools (fig. 69), dense concentrically festooned stratifications resembling those of polished chalcedony or agate (fig. 70). Substantial amounts of organic substance surround densely stratified mineral elements in some regions (textfig. 6 : 5, upper right-hand portion of the diagram, and fig. 71).

Association of these three kinds of microstructures varies in the different parts of the sutures.

As shown in table I, the simplest arrangement, found in the thin cements which separate the nacreous substances of the shell wall and those of the septa consists of a single palisade of tablets, disposed at right angle to the nacreous lamellae, or of two palisades symmetrically disposed along the mural and the septal nacreous layers respectively,

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Textfig. 6. — See figs. 30, 66-71. *Nautilus pompilius* LAMARCK.

Combined drawing showing on the surface of a transverse section of the phragmocone in the region of intersection of the shell wall and of a septum, the different layers, detected with the electron microscope, that fill the angle between the nacreous layer of the shell wall (left) and that of the septum (right).

1. Brick wall assemblage of the aragonite crystals in the nacreous lamellar stratification of the innermost layer of the shell wall;

2. Groups of columnar crystals forming the helle Schicht (figs. 11, 30 and 65), overlapped in some regions by a zone of disturbance in the nacreous architecture (not shown in the drawing) adjacent to the next layer;

3. A layer of amorphous organic substance. Hexagonal and rounded crystals with overgrown smaller crystals are embedded at random in this substance (figs. 66 and 67). Imprints of fibrillar networks (not drawn) were observed occasionally in these strands. Identical layers of varying broadness are shown in the middle and in the upper right parts of the drawing;

4. Palisade of imbricated, sharp-edged, elongated mineral tablets or blades, appearing as irregular girders, needles or spindles in transverse or oblique section (fig. 68). The black needle-like structures aligned in the palisades (also shown in fig. 66) are pseudoreplicas, or fragments of crystals transferred from the original surfaces through the plastic intermediary replica to the final positive metallic replica. Other palisades appear on the right portion of the drawing.

5. Densely stratified parallel mineral elements, here shown in transverse section, disposed in columns, and separated by substantial organic material, constitute one of the heterogeneous structures observed in the regions of the calcareous concretions (fig. 71);

6. Aragonite crystals of the septal nacreous lamellae.

Alternation of organic strands (3) and of palisades (4) varied greatly in the different regions. The present drawing represents two of the combinations (above : 1 - 2 - 3 - 4 - 3 - 4 - 5 - 3 - 6; below : 1 - 2 - 3 - 4 - 3 - 4 - 4 - 6) reported in table 1.

TABLE 2. — Tentative distribution of the mineral and of the organic structures in the *Nautilus* shell.

TYPE OF MINERAL STRUCTURE	ORGANIC STRUCTURES ASSOCIATED WITH THE MINERAL STRUCTURES	TOPOGRAPHY	COMMENTS
Lenticular microcrystals (rounded or with faint hexagonal outlines).		Outer surface of the shell : regions of the umbilical callus and of the adapertural edge. Inner surface of the shell : region near the axis of coiling, region of insertion of the shell muscles (upper surface of the membraneous disc or sole, surface of the shell underlying this sole, adapical and adoral ridges of the muscle scars).	Clustered in considerable numbers in various growth regions *(figs. 2, 4, 7, 10, 12 and 13)*.
Tabular crystals of aragonite (Mother-of-pearl).	Lace-like reticulated sheets of conchiolin (Nautiloid pattern) *(fig. 39)*. Tighter and denser texture in the septa *(figs. 57 and 59)*.	Inner layer of the shell wall. Septa. Regions of nacreous growth : inner surface of the shell (in the living chamber) ; concave adoral surfaces of the free parts of the septa and surfaces of the adapical mural parts of the same (in the phragmocone).	Crystals : mostly tabular hexagones (001) (010) (110), weakly developed along their C-axis (disposed at right angle to the nacreous stratification except in the zones of disturbances), well developed and frequently elongated along their a-axis (predominantly at right angle to the growth lines). (010) plane well developed. Aggregation along (010) or (110) plane. Parallel growth in groups. Moderate overgrowth on their (001) plane of microcrystals (rounded elongated seeds and hexagones) oriented parallel to the a-axis of the underlying crystals *(figs. 3, 8, 9, 45, 46, 47, 50, 51, 55, 56)*.

TABLE 2. — Tentative distribution of the mineral and of the organic structures in the *Nautilus* shell (continued).

TYPE OF MINERAL STRUCTURE	ORGANIC STRUCTURES ASSOCIATED WITH THE MINERAL STRUCTURES	TOPOGRAPHY	COMMENTS
Columnar crystals of aragonite (Mother-of-pearl).		Helle Schicht (hypostrakum).	Variety of mother-of-pearl (W. J. SCHMIDT, 1923-1924) : Crystals more developed along their c-axis than those of regular mother-of-pearl (columnar instead of tabular crystals) *(figs. 11, 28 and 30)*.
Flattened dome-shaped mounds.	Microfibrillar layers of the outer zone *(figs. 33, 34, 36)*.	Outer surfaces of the shell, including those of the flame-like streaks, of the black deposits and of the umbilical region.	Multiple concentric overgrowth of flat crystals (discs) on the (001) plane of underlying crystals *(figs. 1 and 6)*.
Pyramidal or conical mounds.	Septal nacreous reticulated sheets of conchiolin. Posterior membranes of the septa (microfibrillar layers) *(figs. 43, 44, 60-63)*.	Convex adapical side of the septa.	More extensive concentric overgrowth than in the flattened mounds *(fig. 42)*.
Elongated sharp-edged tablets, blades or bars. Aggregates of large lenticular bulging bodies. (Porcellaneous substance.)	Microfibrillar layers and amorphous veils *(figs. 33, 34, 36)*.	Outer and middle portions of the outer layer of the shell wall. Siphonal funnel (inner calcareous ring).	Parallel crystals associated in bundles, plates and oriented very differently in the neighbouring bundles *(figs. 14, 17-19 and 54)*. Crystals disposed radially in corpuscles or in a feather-like arrangement *(figs 17, 18)*.

TABLE 2. — Tentative distribution of the mineral and of the organic structures in the *Nautilus* shell (continued).

TYPE OF MINERAL STRUCTURE	ORGANIC STRUCTURES ASSOCIATED WITH THE MINERAL STRUCTURES	TOPOGRAPHY	COMMENTS
»	»	Inner portion of the outer layer of the shell wall.	Crystals disposed parallel in palisades at the boundary of the inner nacreous layer of the shell wall, at right angle to the (001) plane of the nacreous crystals *(figs. 15 and 27)*.
»	»	Umbilical callus, including the fringes of indentation into mother-of-pearl.	Crystals disposed in bundles, plates, corpuscles, pillars *(figs. 16, 19-21, 25, 26)*. In the fringes of indentation into mother-of-pearl : crystals disposed parallel to the c-axis and at right angle to the (001) plane of the adjacent nacreous tabular crystals *figs. 22-24)*.
As in porcellaneous substance : elongated sharp-edged tablets, blades or bars.	Microfibrils, veils, fibers. Possibly latticeworks *(figs. 18, 79, 82)*.	Sutural cements interposed between shell wall and mural parts of the septa. Extension of these substances in the angles of intersection of the shell wall and of the convex side of the septa.	X-substance (APPELLÖF, 1893) Elongated elements imbricated in palisades *(figs. 66-68, 74) (textfigs. 4, 5, 6)*.
Heterogeneous structures including elongated crystals, rounded corpuscles, thinly stratified amorphous calcareous substance.	»	Calcareous concretions overlapping the X-substance towards the cameral cavities. The mural and septal extensions of these concretions.	Ausfüllungsmasse (APPELLÖF, 1893). Heterogeneous mineral elements disposed at random *(figs. 53, 69, 70) (textfigs. 4, 6)*.
Needle-shaped crystals (Spicules).		Innermost portion of the calcareous ring lining the cavity of the septal funnel.	Brush-like disposition in bundles or faggots (BROOKS, 1888, APPELLÖF. 1893) *(fig. 58)*.

and separated by a central layer of amorphous substance. In the broadest portions of the infillings, fifteen irregularly alternating layers were numbered in some preparations.

In their thinnest wedge-shaped extremities (textfig. 4) the mural parts of the septa appear in cross sections (not shown) as a few parallel nacreous lamellae sandwiched between the palisades of the linear cements on one hand and those of the mural extensions of the sutural infillings, on the other hand. These lamellae are disposed at right angle to the elongated tablets forming the palisades on both sides.

Organic components.

The material of the sutural cements and infillings, dissected from the neighbouring structures and decalcified by chelation, leaves substantial shreds of organic substance. These shreds, thinned by teasing or by ultrasonic disintegration, and deposited on formvar coated screens, appear in the electron microscope as an heterogeneous material, composed of veils (fig. 78) associated with microfibrils, about 6 millimicrons in diameter (fig. 79) and with sturdy fibers (fig. 82). These fibers are either fragments of the posterior membrane intermingled (textfig. 4 : P M) with the septal extensions of the calcareous concretions on the convex side of the septa or remnants of soft tissues previously located in the cameral cavities and subsequently trapped and embedded in the concretions.

IV. — DISCUSSION.

The results of the present observations, summarized in table 2, show that different organic structures, secreted by different portions of the mantle, are associated, in the *Nautilus* shell, with different forms of crystallization of aragonite.

1) Organic components of the shell wall and of the septa.

Two chief organic structures have been observed in the present study in the *Nautilus* shell : reticulated sheets in the nacreous layers of the shell wall and of the septa and relatively scarce microfibrillar material associated with veils in the porcellaneous substance of the outer layer of the wall and of the umbilical callus.

These microfibrils form probably thin sheaths around the elongated crystals characterizing this substance.

Microfibrils were also detected in structures closely related to the shell such as the posterior membrane which coats the convex side of the septa and the crescent-shaped membraneous disc or sole interposed between the shell muscles and the inner shell surface (helle Schicht or hypostrakum).

The organic reticulated sheets of the nacreous portion of the shell wall of *Nautilus pompilius* closely resemble in their structure those described previously in *Nautilus macromphalus*.

In both species, the sheets consist of robust trabeculae, appearing as knobby cords, studded with hemispherical protuberances of various sizes, which separate elongated openings.

These characters constitute the nautiloid pattern, one of the three patterns of structure provisionally recognized with the electron microscope in conchiolin of mother-of-pearl (GRÉGOIRE, DUCHÂTEAU and FLORKIN, 1950, 1955; GRÉGOIRE, 1957).

It is not known, if the reticulated sheets of nacreous conchiolin in *Nautilus macromphalus* and in *Nautilus pompilius* differ with regard to details of structure, such as the disposition and the shape of the openings and the distribution of the protuberances on the trabeculae. This could be established only on the basis of statistical studies of variations of these criteria.

The close similarity or identity in the submicroscopic texture of the reticulated sheets in two of the three surviving species of the genus *Nautilus* so far examined, suggests that the ultrastructural pattern of the nacreous conchiolin in *Nautilus* is representative of the genus and might constitute a stable taxonomic character.

On the other hand, the denser and more slender texture of the septal nacreous reticulated sheets of *Nautilus* associated with the same type of crystallization (tabular crystals of aragonite) as the wall nacreous conchiolin may be explained by the fact that the organic components of the septa are secreted by the posterior region of the mantle, while the nacreous conchiolin of the shell wall is a product of the anterior mantle.

As shown previously (GRÉGOIRE, DUCHÂTEAU and FLORKIN, 1955) successive extractions of protidic and scleroprotidic fractions of the nacreous conchiolin leave residues composed of bundles of polypeptidic fibrils.

In these studies, it had been assumed that the trabeculae of nacreous conchiolin consist of a core of polypeptidic fibrils surrounded in the normal untreated material by a double coating of scleroprotidic substance and of soluble proteins.

Evidence in favour of this interpretation has been supported by various observations on former and on the present material.

Disruption of the sheets and of their trabeculae by protracted ultrasonic irradiation disintegrated the latter into naked fibrils and muffs of substances containing protuberances and bulging rounded bodies of various sizes (GRÉGOIRE, 1960).

After moderate action of ultrasonic waves, which did not disintegrate the lace-like textures, fibrils protruded at the edge of fragmented trabeculae.

Spontaneous disintegration of the sheets into fibrils has also been observed in mother-of-pearl of shells collected in archaeological sites and in fossils (GRÉGOIRE, 1959, 1960).

On the other hand, studies on the structure of the organic sheaths of the prisms of various shells (GRÉGOIRE, 1961) brought evidence that fibrils might also belong to the structure of these sheaths.

Supplemental information obtained in the present study on the fibrillar nature of the organic components of the porcellaneous layer of the shell wall and of the umbilical callus suggests that at least in three different substances involved in the composition of the mollusk shells, mother-of-pearl, prismatic structures and porcellaneous substance, the basic organic ultrastructure of the shells might consist of microfibrils, associated with different other organic components in each of the three substances, and with different types of crystallization of calcium carbonate, aragonite in mother-of-pearl, in the porcellaneous substance and in the prisms of some species, calcite in the prisms of other species.

2. Mineral components of the shell wall and of the septa.

The shell of *Nautilus* consists entirely of aragonite (BÜTSCHLI, 1901; KELLY, 1901; PRENANT, 1926-1927; BØGGILD, 1930) characterized by different forms of crystallization in the porcellaneous substance and in mother-of-pearl.

a) Porcellaneous substance.

The elongated elements observed in the present study in the porcellaneous substance are probably the calcareous fibrils, fibers and needles arranged in columns, bundles and plates variously oriented, described in this substance with the conventional microscope (VON GÜMBEL, 1884; BIEDERMANN, 1902, 1911; W. J. SCHMIDT, 1924; HAAS, 1935; KESSEL, 1935, 1936).

According to APPELLÖF (1893, table XI, fig. 3) the outer layer of the shell wall of *Nautilus umbilicatus* consists of coarse calcareous corpuscles. In his polarisation studies on the same layer, W. J. SCHMIDT (1924) found instead elongated sharp-edged crystals, regularly disposed at right angle to the outer shell surface, at least in the vicinity of the underlying nacreous layer, while in the other parts of the outer layer, the crystals did not exhibit any special orientation.

An irregularly prismatic structure characterizes, according to BØGGILD (1930), the outer layer of the shell wall of *Nautilus pompilius*. The prisms are homogeneous with a feathery arrangement of the axes, which diverge downwards. The upmost portion of the layer is irregularly grained. Downwards, the grains are relatively large and scattered among the prisms.

The present results confirm SCHMIDT's observations with regard to the parallel disposition of the porcellaneous crystals at the boundary of the inner nacreous layer. On the other hand, the large rounded clusters of variously oriented bundles made up of parallel elongated crystals shown in fig. 17, might be the coarse corpuscles of APPELLÖF (1893) and the grains of BØGGILD (1930).

As shown in the present observations, elongated crystals closely similar or identical to those characterizing the porcellaneous substance take part in the constitution of the sutural cements and infillings.

b) Mother-of-pearl.

Coincidence of the limits of the aragonite crystals in successive nacreous lamellae confers to the *Nautilus* mother-of-pearl examined in transverse section a columnar appearance (NATHUSIUS VON KÖNIGSBORN, 1877; BIEDERMANN, 1902; W. J. SCHMIDT, 1924; AHRBERG, 1935 and figs 31 and 31 a of the present paper).

According to SCHMIDT (1923), successive crystal overgrowth taking place in the middle portion of the tabular (001) plane of aragonite crystals belonging to several still growing superimposed lamellae, results in this columnar piling up of crystals which characterizes the *Nautilus* nacreous substance. Evidence in favour of SCHMIDT's interpretation is found in the figs 8, 9, 31, 31 a, 45 and 47 of the present paper, in which overgrown crystals are seen lying in the centre of the tabular plane of basal crystals.

The mounds (figs 1, 5-7) observed on various surfaces and the erected pyramidal or conical structures (fig. 42) detected on the convex sides of the septa seem also to be the result of this particularity of the aragonite crystals in *Nautilus* to superimpose in piles on one another. In these formations, however, the stacking process was limited to solitary basal crystals scattered on the surfaces and did not extend to whole layers as in the regular mother-of-pearl.

Disturbances recorded with the electron microscope in the regularity of the lamellar stratification of mother-of-pearl and resulting from modifications in the normal rhythm of deposition and growth of the aragonite crystals will be discussed in a next section in relation to problems of growth in fossil shells.

On the nacreous growth surfaces in the living chamber and on the concave side of the septa, the crystals of aragonite, variously weathered, were characterized in the material used by the following particularities of structure :

1. Predominance of the hexagonal truncated form of the original orthorhombic prism (W. J. SCHMIDT, 1923) [planes (001) (010) (110)].

2. Predominance of the planes (001) and (010) resulting in tabular shape and elongation of the crystals along their a-axis, especially on the septal concave surfaces.

This orientation of the crystals in the *Nautilus* shell differs from that observed by WADA on the nacreous growth surfaces of shells in Pelecypods (1961), where the crystals exhibit a predominant (110) facet, a (010) facet comparatively small and sometimes absent.

3. As usually on the growth surfaces of mother-of-pearl, orientation of the c-axis of the crystals at right angle to the inner surface of the shell.

Variations in this disposition of the crystals (figs 27 and 32) were recorded in strongly curved portions of the shell (fig. 32) and in the areas of disturbance (fig. 27) in the nacreous stratification (3) including those of the small adapical septa (figs 50 and 51). In the last, rapidly growing structures, orientation of the growing crystals is probably altered in the cavities left between the aragonite crystals belonging to incomplete lamellae already overlapped by newly grown lamellae, and embedded in the stratification.

4. In groups of crystals, growth orientation parallel to their a-axis, disposed at right angle to the direction of the growth lines.

Divergences in orientation, probably related to the shell curvature, were frequently observed in adjacent groups.

Alignment of the crystals along their b-axis, a particularity observed on the nacreous growth surfaces of Pelecypods (W. J. SCHMIDT, 1923-1924; WADA, 1960, 1961) was not recorded on the nacreous growth surfaces of the *Nautilus* shell.

5. Parallel aggregation along (010) and (110) facets, predominantly along the (010) plane of the crystals, on several surfaces.

6. Parallel overgrowth of tabular crystals and of elongated microcrystals (seeds) on the large basal crystals.

In the fields where crystals were disposed at random, parallel overgrowth was observed on the single crystals. Small elements without recognizable crystalline form, appeared elongated in a direction parallel to the a-axis of the underlying crystals.

c) Particularities of structure of aragonite at the layer boundaries.

The layer boundaries are especially interesting because they provide information about the contact alterations undergone by two aragonitic substances — porcellaneous matter and mother-of-pearl — differing in

(3) See also WADA (1961) : Orientation of c-axis varies, not only in different shells, but also in the different layers of the same shell. The layers above and below a resting zone are different in laminary structure *(Pinctada martensii)*.

their type of crystallization and in the structure of their organic components.

As described above, the porcellaneous substance and mother-of-pearl are closely juxtaposed in the shell wall and are especially intricated along the porcellaneous fringes of the umbilical callus, deeply notched within the neighbouring mother-of-pearl.

In the linear sutural cements, the same elongated crystals as those composing the porcellaneous substance are similarly contiguous to mother-of-pearl.

In all these regions examined with the electron microscope in the present study, the porcellaneous elongated crystals were consistently disposed lengthwise, parallel to the c-axis and at right angle to the tabular (001) plane of the nacreous crystals (figs 14, 15, 22-24 and 27).

In the linear sutural cements, this disposition of the porcellaneous elements with respect to the nacreous layers duplicates exactly that found in the shell wall, and seems to subsist in combined structures recorded in the fringes (fig. 22) in which the two types of crystals are associated.

The nacreous lamellae directly adjacent to the porcellaneous substance are frequently altered in their structure and configuration (figs 22, 24 and 27). Alignment of the crystals composing these lamellae is disorganized. Their shape and size vary greatly. Many elements are thicker and more developed along their c-axis than those belonging to the regular nacreous stratification.

A fusion without any distinct boundary between the nacreous lamellae of the shell wall and those of the mural parts of the septa, reported by APPELLÖF (1893, p. 100) and by Mutvei (1957, p. 28) was not observed in the present material. In all parts of the phragmocone investigated, these identical structures never were in contact with one another, and were consistently separated by the sutural cements.

3. Relationships between reticulated sheets of nacreous conchiolin and crystal orientation on the nacreous growth surfaces.

It has long been assumed (ROSE, 1858; KELLY, 1901; KARNY, 1913; SCHMIDT, 1923-1924; WATABE, SHARP and WILBUR, 1958; WADA, 1960, 1961) that the direction of shell and of mantle growth, the nature of the organic matrix (RANSON, 1952) and variations in its production and composition (SCHMIDT, 1923) influence the deposition, the crystallographic form, the growth and orientation of the crystals in the regions of nacreous growth in the mollusk shells.

Detection with the electron microscope of the submicroscopic structure of this nacreous conchiolin in the form of reticulated sheets with three different patterns provisionally recognized (Grégoire, Duchâteau and Florkin 1950, 1955; Grégoire, 1957) made possible the investigation of the problem on an ultrastructural basis.

However, nothing is so far known about the significance of these ultrastructures. As pointed out by Wilbur (1960), the explanation of the fenestration (openings) in the reticulated sheets may well be a problem in the physical chemistry of polymers.

As in other calcifiable tissues (GLIMCHER, 1959; SOBEL, LAURENCE and BURGER, 1960), the organic matrix of conchiolin is certainly involved in induction, orientation and overgrowth of aragonite crystals. However, as pointed out by WILBUR (1960), it is only one of the factors concerned in these processes. Crystal growth in shell can be viewed as a special case of crystallization in solution, and the variation in crystal form within a species is undoubtedly open to interpretation in physico-chemical terms.

Recently, WADA (1960, 1961) reported in Pelecypods *(Pteria, Pinna)* a relation between elongation and tension of the mantle, direction of mantle growth, orientation of the fiber axis of the conchiolin membranes and direction of the b-axis of the crystals of aragonite. WADA assumed that the aragonite crystals developed by epitaxial growth on these organic sheets.

In former investigations (unpublished, 1957) reported here below, the relations between nacreous conchiolin and the overlying crystals were appreciated on natural growth surfaces in the living chamber, on the concave surfaces of the septa (figs 47, 81) and on slightly polished and heavily etched surfaces of still incomplete youngest lamellae (fig. 80). In these lamellae, the crystallographic planes of the crystals of aragonite had not so far been substituted by contact surfaces and could still be recognized.

In such preparations, etching must free only in part the organic matrix, in order to avoid distortions and mechanical displacements of the soft reticulated sheets from their original location with respect to the overlying crystals, while the outlines of these crystals must still remain visible. Such a preparation is shown in fig 80 : the inner nacreous surface of the living chamber of *Nautilus macromphalus* was slightly polished tangentially and subsequently heavily etched. The outlines of two large dissolved hexagonal crystals of one of the youngest lamellae overlay typical reticulated sheets in which the nautiloid pattern of conchiolin is distinctly recognizable. The a-axis of these crystals, which runs obliquely from the lower right to the upper left sides of the figure, is parallel to severai individual trabeculae of the reticulated sheet underlying both dissolved crystals, but shows no obvious relation to other trabeculae (central part of the figure).

A similar coincidence between orientation of a-axis of the overlying crystal and direction of the trabeculae appears in fig. 81.

In spite of negative or equivocal findings, parallel orientation, recorded in several preparations of the nacreous trabeculae and of the a-axis of the overlying crystals suggests that such a relation is probable.

Under these conditions, the divergences noticed in the present study between *Nautilus* and Pelecypods (WADA, 1961) with regard to the shape of crystals (see above), their orientation on the growth surfaces with respect to the growth lines and to the conchiolin trabeculae, might be related to the part played by conchiolin with its taxonomic variations in structure and in chemical composition, as an impurity modifying, as in other mineralizing tissues (habit modification : SOBEL, LAURENCE and BURGER, 1960), the shape, the mode of deposition and the growth of the aragonite crystals.

Impurities may similarly be among the environmental factors responsible for the great differences in the crystal forms and configuration detected in the present material on the surfaces of the concave and of the convex sides of the septa.

As described in a previous section, nacreous growth results on the concave surfaces in development of large hexagonal crystals with parallel orientation in groups, various forms of aggregation, incidental twinning and moderate crystal overgrowth.

On the other hand, on the convex surfaces of the septa, multiple overgrowth resulting in development of conical mounds composed of stacked flat crystals seems to be limited to scattered individual basal crystals.

The nature of the organic background differs on the concave and on the convex surfaces : lace-like reticulated sheets of conchiolin are the predominant and possibly the single organic elements left on the concave surfaces after retraction of the structures of the body mass. On the other hand, on the convex side of the septa, identical reticulated sheets are associated with the microfibrillar layers of the posterior membrane superimposed on to them.

These differences in organic environment between concave and convex surfaces modify presumably the type of crystallization on these surfaces

According to APPELLÖF (1893), the posterior membrane coats initially all the cameral surfaces, but disappears early from these surfaces, except on the convex side of the septa. Under these conditions it could not influence the last steps of crystal growth on the concave surfaces.

4. Organic components of the flame-like coloured streaks, and of the black deposits.

In the absence of biochemical controls, it is not known if the extremely small corpuscles detected in the present observations in the residues of decalcification of the coloured streaks and of the black deposits are related to the actual components of the respective pigments. The significance of the contorted strand-like aggregates formed by the granular material of the coloured streaks is also unknown. This arrangement might result from mere desiccation or might represent the actual disposition of the material scattered between the mineral structures of the outer shell layer. In some replicas, strands similar to those observed in the decalcified sediments were anchored in the grooves between the crystals. However, these structures were difficult to distinguish from the debris of organic shreds of other origins lying on the replicas of the surfaces.

5. The region of insertion of the shell muscles.

The membraneous disc interposed between the mantle lining the shell muscles and the shell has long been described in the literature on *Nautilus* under various, often confusing appellations (horny matter : OWEN, 1832; pellicule charnue, VALENCIENNES, 1841; dicke Conchiliolinplatte, different from the underlying thin Conchiolin substance of mother-of-pearl : WAAGEN, 1867-1870, p. 188; dicke unverkalkte Chitinrinde : APPELLÖF, 1893; cementartige Schicht : THIELE, 1893; conchiolin : CRICK, 1898; Konchinbelag : KESSLER, 1923; LANGE, 1941; Konchinschicht der Basalplatte : M. SCHMIDT, 1925; conchin layer : MUTVEI, 1957).

The structure and the functional significance of this membraneous disc is little known. It plays a role in the adherence of the muscle to the shell and during the forward migration of the muscle associated with the shell growth (THIELE, 1893; VON PIA, 1914).

The literature on the organization of the areas of insertion of the shell muscles in pelecypods and in gastropods does not report (but in *Unio*, THIELE, 1893) the presence of an intermediary substance between the muscles and the inner shell layer on which these muscles are attached.

In spite of extensive investigations, the nature of the connections between the muscle fibrils, the fibrils of the specialized palleal epithelium (« Haftepithel » : TULLBERG, 1882; THIELE, 1893; LIST, 1902; RUBBEL, 1911; RASSBACH, 1912; SIEBERT, 1913; BRÜCK, 1913; RÖCHLING, 1922) and the organic components of the innermost shell layer underlying the muscles, a modified form of mother-of-pearl (« durchsichtige Substanz » : TULLBERG, 1882; EHRENBAUM, 1885; LIST, 1902; « Stäbchenschicht », MÜLLER, 1885; « Hypostrakum » : THIELE, 1893; JAMESON, 1912; BRÜCK, 1913; « helle Schicht » : RUBBEL, 1911; RASSBACH, 1912; SCHMIDT, 1923-1924), is still controversial.

The present study of this region with the electron microscope has provided two fragmentary results.

1. The thinly stratified and cleavable structure of the membraneous disc consists of several layers of extremely small microfibrils. The membraneous material is then thoroughly distinct in its structure from the nacreous conchiolin, though both substances are secreted in the same region of the palleal epithelium (VALENCIENNES, 1841; LEYDIG, 1865; THIELE, 1893) (4).

(4) According to Mutvei (1957), the « epithelial » fibers in Lamellibranchs and Gastropods, and presumably in *Nautilus*, form together a sort of pseudo-tendon between the muscle fibers and the shell. It could not be established, if the layers of microfibrils observed in the present material are this pseudo-tendon.

2. Rounded microcrystals, appearing as lenticular bodies, are gathered in considerable numbers on the surfaces of the membrane and of the underlying shell.

This finding of a considerable proliferation of microcrystals can probably be related to former observations obtained with the conventional microscope.

RÖCHLING (1922) described between the muscle fibers a special category of cells (Kalkspeicherzellen) containing small calcareous inclusions.

HERDMAN and HORNELL (1903), JAMESON (1912), in the Ceylon pearl oyster *(Margaritifera vulgaris)*, and RUBBEL (1911), in the fresh water pearl mussel *(Margaritana margaritifera)* observed numerous minute calcareous depositions or calcospherules, 20 to 500 microns in diameter, developing into pearls, in the muscular tissue and on the surface of the « helle Schicht », along the boundary of the muscle insertions. RUBBEL numbered 400 of these bodies on a surface measuring 2 mm by 2,5 mm.

The relationships between the structures described by these authors and the lenticular bodies gathered in dense clusters, detected with the electron microscope in the areas of muscular insertion or along their boundaries, are not known. The bodies shown in figs 12 and 13 are approximately a hundred times smaller than the smallest corpuscles (« hypostrakum muscle pearls ») described by JAMESON (1912 : Pl. XXXIX, fig. 22 : 20 microns).

These bodies might be the earliest stages of development of the corpuscles described by HERDMAN and HORNELL, RUBBEL, JAMESON, and the cells with calcareous inclusions observed by RÖCHLING might play a part in their constitution.

The intense proliferation of microcrystals in the areas of muscle insertion might represent in the adapical region the steps of fast deposition of new nacreous substance on the adapical areas of resorption left by the most recent forward motion of the muscles during the growth of the shell. Simultaneously, along the adoral ridge of the muscle scars, the clusters of seeds might reflect a specially active secretion of new shell substance induced by particular environmental conditions in close vicinity of the shell muscles.

6. Mechanism of formation of the sutural substances.

Former observations of JAMESON (1912) might bring interesting clues about the mode of development of the sutural cements and infillings and perhaps offer possibility of an experimental approach of the problem.

At the angle of junction between two pearls of *Margaritifera margaritifera* which had become secundarily fused together, JAMESON described with the conventional microscope the structure of a wedge-shaped plug of tissue, developed between the curvature of the surfaces of these two contiguous pearls (JAMESON, 1912 : Pl. XLI, figs 30 and 31).

In this plug, the two chief components of the sutural cements and infillings described above in the *Nautilus* shell can be recognized : 1) parallel needle-like rods disposed in palisades (JAMESON's columnar substance), frequently stratified and consisting of a number of consecutive layers, and 2) an amorphous substance (JAMESON's uncalcified conchiolin) disposed in one or two layers interpolated between the columnar layers.

JAMESON (1912, p. 313) assumed that the following steps occur in the formation of these substances filling the angle between two fusing pearls : addition of fresh nacreous layers on both pearls at the point of contact exerts a pressure on the intervening tissues, consisting of the epithelia of the two pearl-sacs and of a small amount of connective tissue between them. The retreating epithelium ceases to be functional and to control the deposition of its secretion, and is preserved as a membrane. With the shrinkage of the atrophied tissues, a free space occurs into which mineral salts precipitate and organic matter, mixed with these salts, undergoes irregular calcification.

According to JAMESON, the amorphous substance would result from a local epithelial secretion of organic substance at a much greater rate than the lime salts, then would be practically devoid of lime.

At least mechanically similar factors might be involved in the process of formation of the sutural cements and infillings at the intersection of the shell wall and of the septa in the *Nautilus* shell. Other factors such as the exact nature and function of the tissues forming these sutural substances (portions of the mantle; see next section) are insufficiently known.

Development of free spaces resulting from shrinkage of the layer forming tissues, occupied by a liquid phase, might, as suggested by JAMESON, be responsible for irregular calcification such as that detected in the calcareous concretions (infillings : textfig. 6) emerging at the cameral surfaces, as well as for random unoriented development of crystals in organic layers of substance such as those found to alternate with the palisades in the sutural cements (see textfig. 6 : 3 and fig. 65).

However, this tentative interpretation leaves unexplained the mechanism of formation of elongated crystals similar or identical to those of the porcellaneous substance and arranged in palisades, especially between two nacreous layers in the linear sutural cements.

Intermingling of the posterior membrane with the infillings has been reported by APPELLÖF (1893), who observed also that this membrane could overlap these infillings and coat the adjacent parts of the mural surface of the camerae.

In the present observations on dried shells, the relationships between the posterior membrane and the infillings could not be established with certainty. Decalcification of the infillings revealed fibrils and sturdy fibers similar to those forming the microfibrillar layers in the posterior membrane.

7. Submicroscopic structure of the Nautilus shell and test morphology in fossil Nautiloids.

The submicroscopic patterns of nacreous conchiolin preserved in many fossil shells (Grégoire, 1958, 1959 a, b; 1960 a), have already been used for identification, provisionally at the higher levels of taxonomic hierarchy, of nautiloid shell fragments contained in agglomerates composed of crushed material belonging to different taxonomic groups of mollusks (unpublished observations). These fragments were too small to be recognized with conventional criteria.

If the submicroscopic structure of other parts of the *Nautilus* shell presents, like the conchiolin, characters permitting identification, is not known.

The information obtained in the present study will be compared here below with data of the literature on fossil Cephalopoda.

In his important monograph on the nautiloid family *Pseudorthoceratidae*, FLOWER (1939) examined the process of secretion of the various mineral structures of the shell by the different parts of the mantle.

FLOWER distinguished four distinct regions in the mantle of Nautiloidea : *1.* the *terminal mantle*, secreting the shell wall; *2. the posterior mantle*, secreting the septa; *3 and 4.* a *siphonal* and a *cameral* mantles, portions of the posterior mantle, assumed to secrete the annulo-siphonal and the cameral deposits respectively.

1) and 2) : Terminal and posterior mantles.

As pointed out by FLOWER (1939), in forms with regular growth lines and smooth shells, the terminal mantle is active continuously. Crystal deposition and subsequent shell growth proceed at a constant rate throughout the life of the organism.

On the other hand, signs of periodic alternating stages of rest and secretion of the shell were detected in several *Pseudorthoceratidae*, such as *Geisonoceras* and coiled forms of the Devonian (*Cophinoceras* HYATT, *Rhyticeras* HYATT, *Tetranodoceras* FLOWER).

In several of these fossils, the periodicity of rest and secretion resulted in formation of various structures (bands, frills, tubercles, spins and ribs). In *Geisonoceras*, this periodicity in the growth of the shell appears in form of crowding of transverse growth lines at regular intervals corresponding exactly to the distances between the septa (RUEDEMANN, 1921), suggesting that the secretion of the septa coincides with a period of rest in the growth of the animal. Similar observations were made in ammonites (VALENCIENNES, 1841; ARKELL, 1957).

As the process of septation is sudden and discontinuous (PRUVÔT-FOL, 1937, in *Nautilus;* FLOWER, 1939, in fossil Nautiloidea), short periods of secretion alternate with long periods of inactivity of the posterior mantle.

The repercussions of these periodic variations in the growth of the nautiloids on the ultrastructure of the different components of the shell are little known.

Disturbances in the regular stratification of mother-of-pearl, in form of irregular crystals of aragonite, have been incidentally observed with the conventional microscope (W. J. SCHMIDT, 1923).

In permitting recording of variations of limited amplitude, detectable at a submicroscopic level only, of the crystal configuration in the nacreous lamellae of the shell wall and of the septa, the electron microscope might supply information, however indirect, supplementing that provided by the conventional criteria, especially about the nature of the participation of physiological and ecological factors that influence the rhythm of secretion of the shell.

The present observations have shown that the regularity in the stratification of the mural and septal nacreous lamellae was interrupted at periodic intervals by occurrence of thicker lamellae, in which the aragonite crystals were more developed along their c-axis than those forming the adjacent lamellae and exhibited a different orientation.

These disturbances in the nacreous structures reflect alterations in the rate of deposition and in the mode of growth of the crystals. These processes depend themselves, as in other organo-mineral systems (SOBEL, LAURENCE and BURGER, 1960), on variations in composition of the surrounding fluids and possibly of the organic conchiolin structures on to which the crystals developed by epitaxial growth.

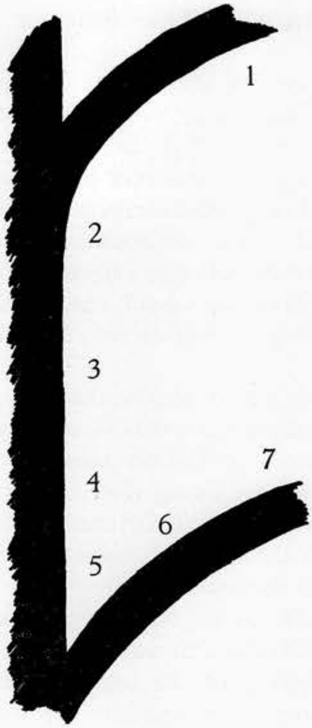
The differences recorded at the electron microscope level between the nacreous structures of the early adapical and of the last adoral septa are in agreement with the reports on the rapid rate of growth of the shell in the neanic age and gradual retardation in the ephebic age, followed by an abrupt retardation in the gerontic stage.

If the synchronic relation of septa to growth lines (RUEDEMANN, 1921) has its counterpart in synchronic modifications in the nacreous stratification of the shell wall and of the septa, has not been investigated in the present study, but appears conceavable.

3) The cameral mantle.

In their explanation of the mechanism of formation of the cameral deposits, TEICHERT (1938) and FLOWER (1939) assumed that a portion of the posterior mantle, the cameral mantle, capable of secreting calcareous material probably in the form of aragonite, would be left behind as the visceral mass moved forward in the conch, and would remain, at least temporarily, linked indirectly to the visceral mass by the siphonal tissues, through the connecting ring (5). This living tissue would

(5) The poor degree of preservation in the dried shells, variously weathered, available in this study, of the soft parts of the siphuncle, did not permit satisfactory observations of these important structures. Fragmentary records on the mineral parts of the septal funnel are reported in the description of results .



Textfig. 7. — Topography of the different types of structures detected with the electron microscope on the cameral surfaces.

1. Iridescent surface of the concave adoral side of the free part of a septum : predominance of large hexagonal crystals (figs. 45 and 46).

2. Iridescent surface of the adapical portion of the mural part of a septum : predominance of large hexagonal crystals, as on the surface of the free part.

3. Lustreless surface of the adoral portion of the mural part of a septum : predominance of rounded mound-shaped eminences, composed of flat superimposed crystals (multiple overgrowth of discs or of lenticular bodies) (fig. 48).

4. Lustreless rugged surfaces situated more adorally than 3 : outcropping (in the form of parallel elongated crystals (fig. 49), of crystals disposed radially (fig. 52) and of small rounded tuberosities (fig. 53) of components of the mural extensions of the calcareous concretions filling the angle of intersection of the shell wall and of the convex side of the septum. According to APPELLÖF (1893), these concretions are coated with the extension of the posterior membrane. Such connections are frequently lost in dried shells.

These mural extensions of the calcareous concretions correspond topographically to the mural portions of TEICHERT's episeptal deposits in fossils (1933).

5. Rugged surface of the infillings which clog the angle of intersection (textfig. 4 : C R).

6. Rugged surface of the septal extensions of the infillings, possibly intermingled with portions of the posterior membrane (textfig. 4 : S E I).

The septal extensions of the infillings correspond topographically to TEICHERT's hyposeptal deposits in fossils (1933).

7. Lustreless brown surface of the convex adapical side of the septum : flat crystals superimposed in conical mounds (multiple overgrowth) surrounded by microfibrillar layers of the posterior membrane (textfig. 4 and figs. 42, 43 and 44).

be responsible for the formation of the cameral deposits in the closed camerae, often far from the living chamber.

Evidence of the tissue itself was found but unfrequently in Nautiloids (see TEICHERT, 1934, FLOWER, 1939).

The findings of the present study on the cameral structures concern the microfibrillar organization of the posterior membrane, which coats the convex side of the septa and the large variety of mineral forms detected in the different parts of the cameral surfaces (textfig. 7). This diversity suggests the existence of different environmental conditions in the deposition and growth of crystals on these cameral surfaces, possibly caused by differences in composition and activity of the portions of the mantle directly involved in production of these structures.

A tentative explanation of the differences in the crystalline structures lying on the convex and on the concave surfaces of the septa has been presented in a preceding section.

The micrographs of both surfaces record a process which had reached a complete standstill for an unknown period of time before the animal died, especially in the early adapical camerae.

Large well defined crystals, such as those found on the concave surfaces, reflect a slowing in the crystal growth on these surfaces before discontinuance. Such large crystals were observed by WADA (1961) on inner surfaces of the shell of *Pinctada martensii* collected in winter.

As the camerae had remained relatively closed until the shell was investigated, outer weathering factors were moderately responsible for the alterations in the crystals consisting of a discrete dissolution in several areas.

The discontinuance of crystal growth on these surfaces might be caused, as in other calcified systems (SOBEL, LAURENCE and BURGER, 1960), by a decreased contact of the crystals with the surrounding organic fluids or by a decreased renewal of these fluids, so that the components for crystal growth were no more available.

The concentric multiple overgrowth of crystals on the (001) plane of basal crystals, resulting in formation of mound-shaped structures, like those found scattered on the convex septal surfaces, has been also observed in the present material in various parts of the outer surfaces of the shell wall, in which the organic substances associated with the mineral components of these surfaces are similarly microfibrillar in structure. However, in these regions, the mounds were rather flattened structures, while many of those detected on the convex side of the septa were much higher.

The development of conical mounds in the closed camerae of the *Nautilus* phragmocone must be specially mentioned because analogous processes take place, as in the *Nautilus* camerae, in closed cavities of other shells, including fossils.

In the lenticular cavities which characterize the shell of the recent family *Aetheriidae* (GRÉGOIRE, unpublished studies), pyramidal structures, consisting of piled crystals scattered over the surfaces of these cavities, are surrounded, as in *Nautilus*, by microfibrillar layers covering the nacreous lamellae.

Another example of pyramidal crystalline complexes developed in closed cavities, however of different crystallographic nature and configuration, is furnished by the pyramids (conellae) composed of several calcite crystals and located in the floors of the hollow keels of some Ammonoidea. These conellae might have developed by diagenetic transformation of a late-formed aragonitic nacreous layer. This layer must have been secreted after withdrawal of the mantle from parts of the primary test (HÖLDER und MOSEBACH, 1950; HÖLDER, 1952; ARKELL, 1957, fig. 136).

8. Submicroscopic structure of the cameral deposits in Pseudorthoceras knoxense (Pennsylvanian).

As it is known, the cameral deposits are calcareous substances developed against the septa and the walls of the adapical camerae in several groups of fossil Nautiloidea. The role of these substances in shell buoyancy and their important significance as a taxonomic criterion have been extensively investigated.

The literature on the cameral deposits has been reviewed in the papers of TEICHERT (1933, 1938) and of FLOWER (1939, 1955). These authors reported the organic origin of these structures, already considered as strongly probable by WOODWARD (1851), by BLAKE (1882, p. 34) by HOLM (1885), and more recently by RUEDEMANN (1906) and TEICHERT (1933).

According to FLOWER (1939), some cameral deposits are composed of aragonitic growth lamellae with vertical or oblique markings, indicative of rows of aragonite prisms, disposed at right angle to the surfaces of secretion. The deposits would be formed by mantle secretion, as are the wall of the conch and the septa.

This description suggests an analogy in structure and organization between these cameral deposits and the sutural substances of the *Nautilus* shell. This analogy has been confirmed recently in a investigation with the electron microscope on cameral deposits of *Pseudorthoceras knoxense*.

In the specimens used in that study, the cameral deposits appeared on the surfaces of polished, transverse and longitudinal sections of the test to be composed of a mosaic of juxtaposed, irregularly shaped, frequently polygonal areas of varying colour and consistency. Gradations with increasing amounts of organic substance were found between milk-white inorganic zones of hard consistency, thinly stratified dark brown regions, composed of alternating festooned, parallel, transversely stratified layers, and, mostly in the central part of the camerae, of soft, dark brown, hardly calcified, crumbly matter (6).

Representative micrographs of different areas of these cameral deposits are shown in figs 72, 73, 75-77.

In fig. 73, on a polished surface of a milk-white calcified zone, closely packed parallel elongated crystals appear without interposition of organic substance. These elements are possibly the secondary deposits of inorganic, and primarily or organic origin, described by TEICHERT (1933).

Bundles or plates variously oriented, composed of parallel elongated tablets and blades, appearing as spindles or rods when viewed on their edges (FLOWER's « aragonite prisms ») (figs 72, 75-77), characterize other regions of the cameral deposits, in which interposition of organic substance between the tablets was confirmed and distinguished from artefacts (replicas of microcracks) by findings of substantial organic material in completely decalcified preparations of the same material.

A striking resemblance with the configuration of the sutural cements and infillings described in *Nautilus* at the angle of intersection of the shell wall and of the septa was found in the stratified dark brown zones of the cameral deposits. As shown in textfig. 8, parallel elongated crystals disposed in palisades alternate, as in the cements of *Nautilus* (textfig. 6), with strands of organic substance. Islands of recrystallization, with smooth surfaces in polished sections, appear embedded in the rows of crystals.

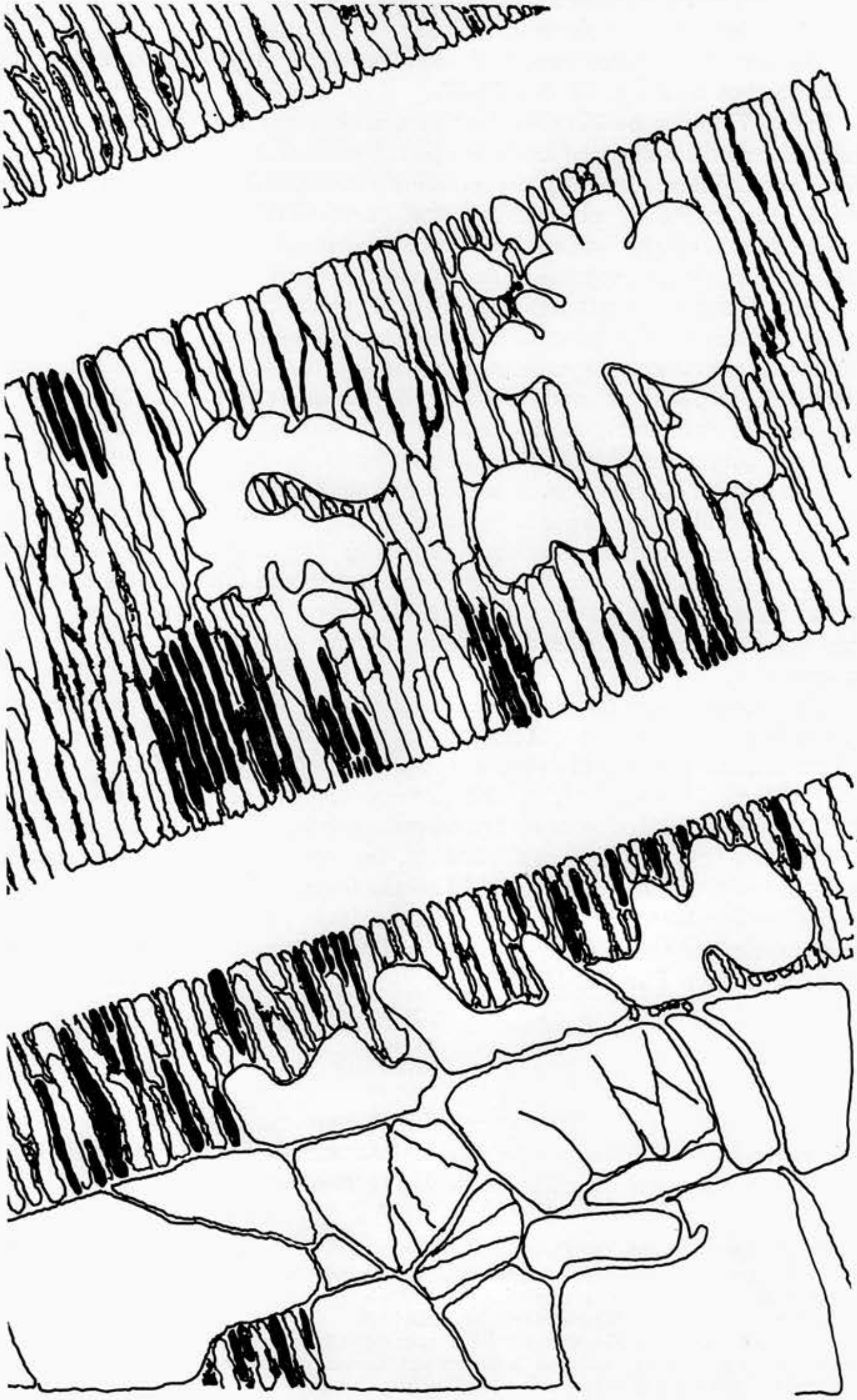
These analogies in structure suggest that the sutural substances, cements and calcareous concretions, of the shell of the recent *Nautilus*, might be, in agreement with a suggestion of BLAKE (1882) (7), the morphological equivalents of the cameral deposits in fossil Nautiloidea, reduced in *Nautilus* to a wedge-shaped material clogging the angle of intersection of the shell wall and of the septa. However, the sutural substances in the *Nautilus* shell fill all the angles of intersection including those of the ultimate camera, while in the fossil phragmocones, an important portion of the adoral camerae is always completely free from these structures (see Flower, 1955).

V. — SUMMARY

1. The submicroscopic structure of the organic and mineral components of dried shells of *Nautilus pompilius* LAMARCK and *Nautilus macromphalus* SOWERBY has been investigated with the electron microscope.

(6) A detailed study of these different regions of the cameral deposits with the phase contrast and with the electron microscopes will be published elsewhere. In the present discussion, only the zones similar in their structure to the sutural cements and infillings of the recent *Nautilus* will be examined.

(7) BLAKE, 1882, p. 35 : « ... the little calcareous infilling of the corner between the septa and the side of the shell is somewhat similar in nature and position to these (mineral deposits) and may have a similar origin. »



2. Approximately 350 different areas of the shell wall and of the septa, in the living chamber and in the phragmocone, have been studied on positive metallic replicas of original surfaces, of surfaces of fracture, of polished transverse and longitudinal sections, before and after etching with chelating agents.

The structure of the organic material has been studied on decalcified fragments of the different regions, thinned by teasing or by disintegration by ultrasonic waves.

3. Various forms of crystals and of crystal aggregates were detected on the outer and inner surfaces of the shell wall and of the camerae.

In the crystals lying on the nacreous growth surfaces of the living chamber, the tabular hexagonal form (001) (010) (110) of the truncated orthorhombic prism of aragonite is predominant.

The c-axis of these crystals is normal to the nacreous stratification, their a-axis, along which many crystals are elongated, is predominantly at right angle to the growth lines.

Parallel orientation and aggregation, parallel overgrowth of microcrystals, oriented along the a-axis of the basal crystals, were recorded in groups of neighbouring crystals but orientation differed in other adjacent groups.

Orientation of the crystals with their a-axis parallel to the direction of the trabeculae of the reticulated sheets of conchiolin on which these crystals had developed by epitaxial growth, was observed in some preparations, but was not obvious in others.

The present conclusions about the structures of the weathered surfaces will be amended when fresh shells will be available.

4. The membraneous disc or sole, interposed in the living chamber between the muscles and the shell wall, is composed of stratified, cleavable layers of thin microfibrils arranged in dense feltings.

Near the adoral and adapical ridges of the muscle scars, globular or lenticular microcrystals, clustered in considerable numbers, are scattered

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Textfig. 8 (compare with textfig. 6). — *Pseudorthoceras knoxense* Mc Chesnay (Pennsylvanian). Polished and etched (titriplex III : 3 min.) surface of a sagittal section of the test. Dark brown, thinly stratified region of the cameral deposits.

The drawing shows alternation of layers appearing as amorphous strands on the surfaces (in white) and of layers composed of parallel imbricated, elongated tablets, blades or bars, disposed in palisades, at right angle to the length of the layers.

Comparison with Textfig. 6 shows the close resemblance of these structures and of their configuration in the cameral deposits with those of the sutural substances of the recent *Nautilus*, especially the milk-white cements.

Irregularly shaped mineralized islands, with smooth or finely granular surfaces, are probably zones of recrystallization (see Teichert, 1933) scattered at random, that have invaded (bottom left) broad areas where they have replaced the original structures.

over the surface of this membranous disc and over that of the underlying shell wall, composed of a variety of mother-of-pearl (helle Schicht).

The number of these microcrystals, estimated in several fields, varied between 2 and 126 millions per square millimeter of surface.

5. The surfaces of the concave and of the convex sides of the septa differ greatly in their structure.

On the concave side, large, mostly hexagonal tabular crystals (001) (010) (110), elongated along their a-axis, are lying on the youngest nacreous lamellae and partly embedded in conchiolin sheets.

On the convex side, conical or pyramidal structures, composed of stacked discs, are scattered among shreds of the posterior membrane.

6. The posterior membrane which coats the convex side of the septa is composed of microfibrillar layers.

7. The basic mineral structure representative of the porcellaneous substance in the outer layer of the shell wall and in the umbilical callus, consists of mostly elongated, sharp-edged tablets, blades, plates or bars, appearing in transverse or oblique sections, in the form of girders, beams, rods, needles or spindles.

These elements are generally assembled in bundles, plates, rows or corpuscles. The composition of these groups, which varies in the different porcellaneous regions, is described.

At the border line of porcellaneous and nacreous substances in the shell wall, the elongated elements are predominantly parallel to the c-axis of the nacreous crystals, and normal to the nacreous stratification.

An identical disposition was detected along the fringes of porcellaneous substance deeply notched in the neighbouring nacreous substance, in the region of the umbilical callus and in the sutural substances.

The organic sheaths interposed between the elongated porcellaneous elements of the outer layer of the shell wall and of the umbilical callus are composed of microfibrils associated with veils.

8. Particularities of structure characterizing the nacreous layers of the shell wall and those of the septa are described. Periodic disturbances in the stratification of the nacreous lamellae consist of variations in the growth along their c-axis and in the orientation of the aragonite crystals involved in the structure of the lamellae.

Differences in the crystal shape, size and disposition between the early adapical and ultimate adoral septa reflect differences in the rate of crystal growth of the respective formations.

These findings suggest the possibility of extending the physiological and morphological studies of the periodicities in the shell growth to a submicroscopic level.

9. In *Nautilus pompilius*, the pattern of the lace-like reticulated sheets of nacreous conchiolin of the shell wall is closely similar or identical to

that detected previously in *Nautilus macromphalus*. This pattern of structure of nacreous conchiolin (« nautiloid pattern ») found in two of the three surviving species of the living genus *Nautilus* appears to be a reliable taxonomic character.

The septal nacreous conchiolin differs by its tighter texture and by its more slender trabeculae from that of the shell wall.

10. In the areas of junction of the septa and of the inner surface of the wall, the mural and septal nacreous substances are not contiguous. Layers of calcareous substance, with a structure thoroughly different from mother-of-pearl, are interposed in between.

These substances, or sutural infillings, include :

1) the linear milk-white cements sandwiched between the shell wall and the mural parts of the septa,

2) the extensions of this material which clog the angles of intersection of the wall and of the convex sides of the septa,

3) the calcareous concretions which overlap the angular infillings and protrude into the cameral cavities.

These substances, especially the cements, are composed of layers made up of parallel imbricated, elongated crystals, disposed transversely in the layers. The layers alternate with strands of organic amorphous substance.

The elongated crystals are identical to those which characterize the porcellaneous substance.

The organic material interposed between these crystals is similarly composed of microfibrils and veils.

The calcareous concretions protruding into the cameral cavities are characterized by a disorderly amalgamation of bundles of crystals and of densely stratified sheets of amorphous mineral substance, in which substantial organic matter is embedded.

11. The findings collected with the electron microscope are discussed with reference to particularities of the test configuration in fossil *Nautiloidea* reported in literature.

A comparative study of the sutural infillings of the recent *Nautilus* shell and of the cameral deposits of *Pseudorthoceras knoxense* has revealed close similarities in the structure of these two kinds of substances.

It is assumed that the wedge-shaped plug of calcareous substance which fills the angles of intersection of the shell wall and of the convex sides of the septa in the recent *Nautilus* might be the morphological equivalent, confined to a restricted area, of the cameral deposits of fossil Nautiloidea.

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EXPLANATION OF PLATES.

1. Positive carbon replicas (double stage method) shadow cast with palladium, of the outer and of the inner surfaces of shells, in the living chamber and in the phragmocone.

2. Positive carbon replicas of regions of fracture and of polished and etched sections of the shell wall and of the septa (Etching time indicated in brackets).

3. Organic structures, decalcified with chelating agents, deposited on formvar films, some after disintegration or cleavage by ultrasonic waves, and shadow cast with palladium, of the outer porcellaneous and of the inner nacreous layers of the shell wall, of the septa, of the flame-like coloured streaks, of the black deposits, of the posterior membranes of the septa and of the membraneous disc underlying the shell muscles.

The figures are prints made from the original negative (white shadows generally directed towards the upper or upper right side of the figures), and reversed prints, obtained through intermediary direct prints on plates (black shadows generally directed towards the lower and the lower left sides of the figures).

PLATE I.

Nautilus pompilius LAMARCK.

Figs 1 and 6.

Surface of the umbilical region. Boundary between the black deposits and the crescent-shaped iridescent nacreous area overlapping these deposits on the outer surface of the last whorl.

Fig. 1 : two dome-shaped elevations are composed of superimposed flat rounded crystals in the form of discs. The piling up of the crystals is indicated by the undulating white fringes surrounding the slopes of the mounds.

Fig. 6 represents a less advanced stage of development of the dome-shaped elevations. Approximately five superimposed discs are recognizable.
Reversed prints. Fig. 1 : × 9.000; Fig. 6 : × 22.000.

Figs 2 and 7.

Surface of the crescent-shaped iridescent area in the umbilical region.

Globular microcrystals and their pseudoreplicas are clustered on the surfaces in this field. These pseudoreplicas, appearing as white rounded or polygonal bodies on the reversed prints, are crystals torn off from the original surface, which adhered to the intermediary plastic negative replica, were then covered with carbon to which they remained attached, when the intermediary replica was dissolved.

Shreds of organic substance (white strings) surround the crystals.

In fig. 7, enlarged portion of fig. 2, the blurred hexagonal outlines of some crystals are recognizable (upper right corner of the figure).
Reversed prints. Fig. 2 : × 14.500; Fig. 7 : × 22.000.

Figs 3 and 5.

Inner nacreous surface of the shell wall in the living chamber, a few millimiter in adoral direction outside the adoral ridge of the muscle scars.

Fig. 3 shows a tabular hexagonal crystal or aragonite (001) (010) (110) with its a-axis directed towards the upper right side of the figure. Elongated microcrystals scattered on the (001) plane of this crystal are all oriented parallel to its a-axis. Similarly oriented microcrystals appear on crystals of the underlying lamella.

Fig. 5 shows overgrowth with parallel orientation of an hexagonal tabular crystal on another hexagonal crystal.

On the inner surfaces of the shell in the living chamber, development of the overgrowth process gave rise to the crystal arrangement shown in fig. 9 and, on the outer surfaces, to the mound-shaped structures shown in figs 1 and 6.

Reversed prints. Fig. 3 : × 22.000; Fig. 5 : × 22.000.

Fig. 4.

Inner lateral nacreous surface of the shell wall, near the axis of coiling, about 10 millimeter in adoral direction, outside the adoral edge of the area of insertion of the shell muscles.

The figure shows approximately seventeen small crystals, with rounded or blurred hexagonal outlines, and two pseudoreplicas (black rounded bodies) of similar crystals. The crystals are disposed at random, without any relation to the direction of the growth lines, which are parallel to the width of the figure.

Groups of seeds lying on the background between the crystals are visible in the middle portion of the figure.

Direct print : × 12.500.

PLATE II.

Nautilus pompilius LAMARCK.

Fig. 8.

Inner nacreous surface of the shell in the living chamber (median plane).

Six hexagonal tabular crystals oriented parallel to their a-axis and the outlines of crystals belonging to the underlying incomplete nacreous layers are shown in this field. As in fig. 3, the (010) plane of these crystals is well developed. In the middle part of the figure, elongated microcrystals appear oriented parallel to the a-axis of a crystal belonging to the underlying layer.

Direct print : × 14.500.

Fig. 9.

Inner lateral nacreous surface of the shell wall in the living chamber, outside the adoral ridge of the muscle scars.

Crystal aggregation, parallel orientation and parallel overgrowth are shown in about seven groups of tabular hexagonal crystals with their (010) plane well developed.

About five superimposed layers of crystals are visible in some groups. This disposition reflects the simultaneous growth of several still incomplete lamellae. The undermost layer is a nacreous lamella near completion. Numerous weathered microcrystals are scattered over all the surfaces. Some of these microcrystals are elongated and oriented parallel to the a-axis of the basal crystals.

Reversed print : × 14.500.

Fig. 10.

Inner lateral nacreous surface of the shell wall in the living chamber, near the adoral edge of the muscle scars.

In this preparation, the direction of the nacreous growth lines is parallel to the width of the figure.

About three parallel rows of microcrystals are shown. The a-axis of these microcrystals, where recognizable, and that of the larger hexagonal crystal shown in the upper right portion of the figure are oriented nearly at right angle to the direction of the growth lines.

Similar groups of microcrystals were gathered on the nacreous surfaces between areas (not shown) characterized by multiple overgrowth of large tabular crystals. Pseudoreplicas of crystals appear as rounded or hexagonal black circles.

Direct print : × 31.000.

PLATE III.

Fig. 11.

Inner shell surface in the region of insertion of the muscles, in the living chamber.

This figure illustrates the considerable disturbance undergone by the innermost nacreous layers under the influence of the muscle traction, a factor responsible, according to W. J. SCHMIDT (1923), for the particular structure of the helle Schicht or hypostrakum.

As established by W. J. SCHMIDT on the basis of polarisation studies (1923), the helle Schicht represents a variety of mother-of-pearl, in which the nacreous aragonite crystals are considerably more developed along their c-axis than the tabular crystals aligned in rows in the ordinary nacreous stratified lamellae, and appear in the form of columns, elongated girders or beams, disposed parallel in bundles resembling sturdy pillars. In this preparation, several bundles of crystals are erected or collapsed in various orientations on to the background. On the brightly illuminated top surfaces of these pillars, which correspond to the original innermost surface of the shell facing the mantle and the muscle, the extremities of the parallel columnar crystals are distinctly visible.

Direct print : × 9.000.

Fig. 12.

Inner surface of the shell wall. Adapical edge of the area of insertion of the shell muscles.

Rounded or hexagonal microcrystals of various sizes (from 15 millimicrons to 1 micron) and shapes are scattered on the surface without any distinct orientation.

Reversed print : × 14.500.

PLATE IV.

Nautilus pompilius LAMARCK (Figs 13, 15 and 16).

Nautilus macromphalus SOWERBY (Fig. 14).

Fig. 13.

Inner surface of the shell wall, Adapical edge of the area of insertion of the shell muscles.

In this field, the mineral surface is covered with lenticular or globular microcrystals. From counts on prints of this area, the number of microcrystals was estimated to amount to 126 millions per square millimeter of shell surface.

Reversed print : × 25.000.

Figs 14 and 15.

Polished and etched (Fig. 14 : 25 sec.; Fig. 15 : 3 min.) transverse sections of the shell wall in the phragmocone.

Fig. 14 : Boundary of the outer porcellaneous (right) and of the inner nacreous layers (left). On the left side of the figure, the parallel stratification of the nacreous lamellae is interrupted by a wedge-shaped indentation of porcellaneous substance. This substance consists of parallel elongated, imbricated, sharp-edged tablets, blades, bars or flattened rods, disposed at right angle to the nacreous lamellae. In the right portion of the figure, similar parallel elements are grouped in bundles or plates in which the crystalline components are oriented at different angles with those of the adjacent groups. About nine groups are shown, in which the elements appear in transverse, oblique or longitudinal section in the plane of polishing. The black bodies scattered in the middle part of the figure are pseudoreplicas of fragments of elongated crystals.

Direct print : × 9.000.

Fig. 15 : Boundary of the innermost portion of the porcellaneous layer and of the nacreous layer in the shell wall. In this region, parallel elongated, imbricated tablets of the porcellaneous substance (left) are most frequently disposed in palisades at right angle to the rows of aragonite crystals forming the nacreous lamellae (right), either directly, or, as shown in the figure, with interposition of pebble-like corpuscles.

Reversed print : × 14.500.

Fig. 16.

Polished and etched (100 sec.) transverse section of the umbilical callus.

The elongated elements characterizing the porcellaneous substance are here shown associated into an arborized structure diverging from a central stem.

Direct print : × 10.000.

PLATE V.

Nautilus pompilius LAMARCK.

Figs 17 and 18.

Polished and etched (60 sec.) transverse sections of the outer portion of the porcellaneous layer of the shell wall.

Fig. 17 shows the composition of a large corpuscle, about 6 microns in size, corresponding presumably to one of the « coarse corpuscles » described with the conventional microscope by APPELLÖF (1893).

The basic mineral units found in this formation consist of parallel elongated elements assembled in about seven groups, in which the crystals are disposed at very different angles to those of the adjacent groups (fig. 17). Within the groups, the elements are either disposed radially (lower left part of fig. 17, and fig. 18) or are parallel imbricated and arranged in bundles. In the upper right portion of the composed corpuscle (fig. 17), the etched extremities of the elements, seen in transverse or oblique section in the plane of polishing, appear as a mosaic of rounded pebbles. In the lower left part of fig. 17, and in fig. 18, the elements of the radiating structures branch laterally into fan-shaped arborized expansions diverging from a central stem, similar to those shown in Plate 4, fig. 16.

Reversed prints. Figs 17 and 18 : × 19.000.

Fig. 19.

Polished and etched (3 min. 25 sec.) transverse section of the umbilical callus.

The figure shows in the middle part of the porcellaneous substance a group of parallel, elongated and imbricated elements (with their pseudoreplicas in black) notched like a wedge into two other groups of parallel tablets with a different orientation.

Direct print : × 7.000.

PLATE VI.

Nautilus pompilius LAMARCK.

Fig. 20.

The figure shows a representative portion of a surface of fracture (unetched) of the porcellaneous substance in the umbilical callus.

Three large spindle-shaped systems appear subdivided into a mosaic of rounded or square superimposed fields, disposed in vertical lines which diverge downwards in a feather-like fashion. The bulging surfaces of these square fields correspond possibly to the plane of transverse fracture of elongated crystals, and the large spindle-shaped systems to groups of these elements such as those illustrated in figs 17 and 21.

Reversed print : × 9.000.

Fig. 21.

Polished and etched (60 sec.) transverse section of the middle portion of the umbilical callus.

Several pillars composed of parallel, elongated, sharp-edged tablets are shown. The size of these tablets varies greatly : some of these elements appear (centre of the figure) as small rectangular bodies.

Reversed print : × 19.000.

Figs 22 and 23.

At the boundary of the umbilical callus and of mother-of-pearl, extremely thin, milk-white, undulating fringes of porcellaneous substance, distinctly visible at low magnification on transverse polished sections of this region, send deep indentations into the brown yellowish nacreous substance.

Figs 22 and 23, polished and etched (60 sec.) transverse sections of these regions, show two aspects of the interpenetration of the porcellaneous and nacreous substances.

Portions of fringes appear sandwiched between two nacreous areas, recognizable by their lamellar stratification. Conchiolin sheets alternating with mineral lamellae, revealed by etching and collapsed on to the underlying surfaces, appear as parallel thick pads.

In fig. 22, a nacreous crystal shown in transverse section seems to be soldered without visible demarcation, with an elongated, club-shaped element of the porcellaneous substance. Three small, roughly square expansions are attached to this element on its right side. Farther right and on the left of the club-shaped element, porcellaneous tablets are disposed at right angle to the nacreous lamellae (below). In the upper part of the figure, other nacreous lamellae seem to have been driven back and compressed by the development of the club-shaped crystal. In fig. 23, the porcellaneous elongated tablets, some involved only in part in the plane of polishing, appear distinctly disposed at right angle to the nacreous lamellae of the upper and of the lower parts of the figure.

Direct prints. Figs 22 and 23 : × 19.000.

PLATE VII.

Nautilus pompilius LAMARCK.

Fig. 24.

See legends of Plate 6, figs 22 and 23.

Polished and etched (60 sec.) transverse section of the umbilical callus. Boundary of mother-of-pearl and of a porcellaneous fringe radiating from the callus into the substance of the crescent-shaped nacreous layer overlapping the callus near the axis of coiling of the last whorl.

Near the boundary of these two substances, the regular parallel stratification of the nacreous lamellae (upper right part of the figure) is disturbed.

About 2 cm above the black pseudoreplica, a nacreous crystal, thicker than the adjacent crystals of the same lamella, sends two oblique expansions into the next lamella below. Further down, in the last nacreous rows, the tabular crystals are no more recognizable and are replaced by corpuscles of ill defined shapes and sizes. Below this area of nacreous disturbance, the imbricated elongated elements characterizing the porcellaneous substance are arranged in palisades, at right angle to the nacreous stratification.

Direct print : × 12.500.

Figs 25 and 26.

Polished and etched (60 sec.) transverse sections of the umbilical callus.

Fig. 25 : Details of structure, revealed by etching, of the components of the porcellaneous substance.

In this area, juxtaposed bulging lenticular bodies appear grouped into larger corpuscles disposed at random. White strings separating the bodies and the groups of bodies, are either artifacts of replication (metallic replicas of cracks) and/or organic substance sandwiched between the mineral components.

Reversed print : × 25.000.

Fig. 26: The roof-like oblique imbrication of elongated sharp-edged tablets, juxtaposed with, or composed of bulging lenticular bodies is shown. At the lower right corner of the figure, a typical elongated porcellaneous tablet is visible in tangential orientation.

Reversed print : × 25.000.

PLATE VIII.

Nautilus pompilius LAMARCK.

Fig. 27.

Polished and etched (60 sec.) transverse section of the shell wall in the living cham ber, showing the boundaries of the inner portion of the outer porcellaneous layer (upper fourth of the figure) and of the inner nacreous layer (three lower fourths ol the figure).

In mother-of-pearl, three groups of stratified thin lamellae composed of 6, 7 and 6 rows of flat tabular crystals respectively from bottom to top, alternate with two thick lamellae, differently oriented and appearing in the figure as steep oblique cliffs.

At the limit of the porcellaneous and nacreous zones, the brick wall disposition of the nacreous aragonite crystals is disturbed. Isolated tabular crystals (upper left) are intricated with corpuscles belonging to the porcellaneous layer. In the latter layer, several elongated tablets appear distinctly disposed at right angle to the nacreous stratification.

Direct print: × 22.000.

Fig. 28.

Polished and etched (100 sec.) transverse, slightly oblique section of the innermost part of the shell wall of the living chamber in the adapical portion of the region of muscle insertion.

A former hypostrakum or helle Schicht appears embedded in mother-of-pearl grown upon it after the muscle moved forward in the shell. In the portion of this layer here shown, the crystals are four to five times higher than those of the adjacent lamellae. Fragments of reticulated sheets of conchiolin are seen collapsed on to the columnar crystals (right part of the figure).

Direct print: × 22.000.

PLATE IX.

Nautilus pompilius LAMARCK (Figs 29, 30 and 32).

Nautilus macromphalus SOWERBY (Figs 31 and 31 a).

Figs 29 and 32.

Surface of fracture of the shell wall near the axis of coiling, showing the configuration of the nacreous lamellar stratification in a curved region of the wall.

In fig. 29, the broken edges and a portion of the surfaces of approximately 20 successive lamellae are shown. Differences in the length of shadows reveal variations in orientation of groups of lamellae. Debris of nacreous reticulated sheets (white shreds or strings) appear scattered on the surfaces of the lamellae and sandwiched between them.

In fig. 32, a crystal with imprints of shreds of conchiolin on its tabular (001) plane, slightly oblique to the plane of the figure, lies in close vicinity of other crystals (below) disposed nearly at right angle to it.

Reversed prints. Fig. 29: × 6.500; fig. 32: × 22.000.

Fig. 30.

Polished and etched (100 sec.) transverse section of the innermost part of the shell wall in the region of muscle insertion in the living chamber (see fig. 28).

In the columnar crystals of a young helle Schicht, etching reveals lenticular bodies, probably components of the inner structure of the crystals. In the lower portion of the figure, the rectangular outlines in transverse section of aragonite crystals (pseudoreplicas) belonging to the regular structure of the underlying mother-of-pearl are shown.

Direct print : × 16.000.

Figs 31 and 31 a.

Polished and etched (4 min.) transverse sections of the nacreous layer of the shell wall in the living chamber, showing zones of disturbance, in the form of thicker lamellae, in the nacreous stratification (compare with fig. 27). Shreds of nacreous conchiolin appear on the upper part of the crystals as white strands folded downwards over the plane of polishing. The c-axis of the large crystals in the altered lamella is about three times that of the crystals of the other lamellae. As this part of the shell was located adorally to the area of muscle insertion, the alterations here shown are unrelated to the presence of muscles. The margins of the large tabular crystals coincide in seven successive lamellae, and crystals are piled up in columns, a particularity of the nacreous structure in the *Nautilus* shell, shown also in fig. 31 a.

Fig. 31 : Reversed print : × 16.000; Fig. 31 a : direct print : × 14.400.

PLATE X.

Nautilus pompilius LAMARCK.

Figs 33, 34 and 36.

Decalcified milk-white coloured dust, exposed to ultrasonic waves, from filed porcellaneous layer of the shell wall (living chamber).

The residues consisting of fibrils associated with or embedded in thin veils (fig. 34) appear scattered on the supporting films.

Reversed prints. Figs 33 and 34 : × 31.000; fig. 36 : × 38.000.

Figs 35 and 37.

Decalcified yellow dust from filed tinted portion of the outer porcellaneous layer of the shell wall, in the region of the flame-like streaks.

Procedure of preparation as in fig. 33.

The residues of decalcification consist of small particles aggregated into rounded bodies or into contorted strands.

Direct print. Figs 35 and 37 : × 26.000.

Fig. 38.

The substance of the black deposits collected on the surface of the phragmocone, decalcified and exposed to ultrasonic waves, furnished homogeneous suspensions of small particles, 3 millimicrons in diameter, and shown in this figure agglutinated in dense clusters on the supporting film.

Direct print : × 52.000.

PLATE XI.

Nautilus pompilius LAMARCK.

Fig. 39.

Soft iridescent membrane of conchiolin from decalcified mother-of-pearl (inner layer of the shell wall in the living chamber), immersed in 2 per cent osmium tetroxide for 28 hours and exposed to ultrasonic waves.

Drops of the strongly iridescent aqueous suspensions of this material were deposited on supporting formvar films, drained, dried after sedimentation of the shreds of substance, coated with a thin film of carbon evaporated at normal incidence, and shadow cast with palladium. The formvar supporting film was then dissolved.

The fragments of lace-like reticulated sheets here shown result from the ultrasonic cleavage and breakage of the conchiolin membranes. With the procedure used, these fragments are actually hanging underneath the double, carbon and palladium, metallic coating (see GRÉGOIRE, 1960).

The characters of the « nautiloid pattern » of structure are recognizable in these fragments : sturdy, irregularly cylindrical trabeculae or cords, studded with numerous hemispherical protuberances of various sizes, separate elongated openings of irregular outlines.

Reversed print : × 43.000.

PLATE XII.

Nautilus pompilius LAMARCK.

Figs 40 and 41.

Membraneous disc (muscle sole) interposed between the shell muscles and the inner surface of the shell, cleaved with tweezers into transparent semi-rigid, plate-shaped shreds. These shreds were fixed directly on formvar films (fig. 40), or were first disintegrated by exposure to ultrasonic waves. Drops of their aqueous suspensions were deposited on formvar films (fig. 41).

Fig. 40 shows in a thin region of cleavage at the edge of a thicker shred (extreme right) a layer composed of densely parallel stretched microfibrils. In fig. 41, the fibrils and groups of fibrils associated in fibers, are scattered on the supporting film. The broad white bands are folds in the formvar film.

Fig. 40 : direct print : × 47.000; fig. 41 : reversed print : × 22.000.

Fig. 42.

Surface of the adapical convex side of the last septum, forming the floor of the last camera.

One of the scattered conical or pyramidal eminences erected on the surface is shown.

This structure is composed of flat rounded crystals stacked upon one another like pancakes. The blurred limits of these crystals are visible as undulating white fringes around the steep slopes of the cone. All the stages of overgrowth were found on the convex surfaces between systems composed of two superimposed flat crystals (see plate 1, fig. 5) with a bulging (001) plane, and the structure here shown, in which about 10-12 crystals are piled up. Debris of the microfibrillar layer composing the posterior membrane of the septum are visible as scattered granulations on the background surrounding the cone (see fig. 43 and fig. 44).

Reversed print : × 38.000.

Figs 43 and 44.

Surfaces of the convex side of one of the early adapical septa.

The microfibrillar structure of the posterior membrane which coats the mineral surfaces of the convex sides is shown in direct (fig. 43) and in reversed (fig. 44) prints.

Compare with figs. 60-63.

Fig. 43 : × 43.000; fig. 44 : × 31.000.

PLATE XIII.

Nautilus pompilius LAMARCK.

Fig. 45.

Slightly etched (10 sec.) concave adoral surface of the last but one septum.

Parallel oriented growth, parallel overgrowth, aggregation predominantly along their (010) plane, are shown in groups of hexagonal tabular crystals elongated along their a-axis and with their (010) plane well developed. In the lower right part of the figure, four layers of superimposed crystals are visible.

In the upper group, orientation of one crystal differs from that of the other groups shown in the figure (see textfig. 2).

Direct print : × 4.000.

Fig. 46.

Concave adoral surface of the last but five septum.

Large hexagonal tabular crystals are surrounded by and partly embedded in conchiolin shreds with the characteristic nacreous lace-like reticulated structure. Fig. 46 represents a portion of an area of the surface in which the crystals are oriented along two parallel curved lines.

Direct print : × 4.000.

PLATE XIV.

Nautilus pompilius LAMARCK.

Fig. 47.

Concave adoral surface of the last but eight septum.

Parallel overgrowth and aggregation are shown in two groups of truncated hexagonal crystals elongated along their a-axis. The planes of the basal crystals underlying these two groups are visible only in part. Orientation of elongated small seeds (upper left part of the figure) coincides with the a-axis of the upper group of overgrown crystals. On the other hand, orientation of the a-axis of the large crystal and of the microcrystals lying parallel to this a-axis on its (001) plane, seen at the upper right part of the figure, differs by 58° from that of the two groups of overgrown crystals described above.

In the left lower corner of the figure, trabeculae of reticulated sheets of conchiolin are oriented parallel to the a-axis of the two adjacent groups of overgrown crystals.

Reversed print : × 9.000.

Fig. 48.

Mural adoral surface of one of the adapical camerae, adoral prolongation of the mural surface of a septum (textfig. 4 : region below SM).

In this region, the large tabular hexagonal crystals which characterize the concave surfaces of the free parts and the beginning of the mural parts of the septa were not found. Instead, large rounded or oval bulging structures, with an upper plane composed of a mosaic of flat lenticular microcrystals are representative of these surfaces. This disposition suggests the development in this area of multiple overgrowth of flat lenticular crystals, resulting, as on other surfaces of the shell, namely the convex side of the septa, in formation of mound-shaped structures (top left of the figure). In the field here shown, the mineral structures had undergone partial dissolution.

Reversed print : × 14.500.

Fig. 49 (see textfig. 4, MEI, and figs 52 and 53).

Surface of the wall of the last adoral camera, in the adoral prolongation of the region shown in fig. 48, and in the vicinity of the angle of intersection of the wall and of the convex side of the ultimate septum.

In this region of the mural surfaces of the camerae, as shown in textfig. 4 (MEI), extension of the calcareous substances filling the angle of intersection of the wall and of the convex side of the next adoral septum conceals the mural extensions of the preceding adapical septum (textfig. 4 : SM). Parallel elongated and possibly imbricated tablets crop out at the cameral surface.

These structures which are involved in the composition of the sutural infillings resemble those described in the porcellaneous layers (see the text).

Direct print : × 16.000.

PLATE XV.

Nautilus pompilius LAMARCK.

Figs 52 and 53.

(See Plate 14, fig. 49, and textfig. 4 : MEI).

Surface of the mural extension of the calcareous deposits in the last adoral camera, in the region of intersection of the shell wall and of the convex side of the ultimate septum.

Fig. 52 : A radial disposition of crystals emerging as a polygonal area at the surface of the calcareous deposits.

Fig. 53 : rugged surface consisting of rounded stacked eminences (microcrystals ?), some of them exhibiting faint hexagonal outlines. Presence of microcrystals in this area could reveal the last steps of growth before standstill, of the calcareous concretions protruding into the cameral cavities.

Direct prints. Fig. 52 : × 16.000; Fig. 53 : × 22000.

Figs 50 and 51.

Polished and etched (30 sec.) transverse sections of mother-of-pearl in two thin septa of the adapical region of the phragmocone.

In both figures, especially in fig. 50, particularities in the nacreous lamellar stratification, such as irregular orientation of the crystals forming the rows, variations in thickness of these crystals, predominance of small rounded pebble-shaped crystals in some rows, alternation of thick and of thin lamellae at irregular intervals, might indicate a rapid growth rate of these early septa with transitory slowings revealed by the presence of relatively thicker lamellae.

Reversed prints. Fig. 50 : × 22.000; fig. 51 : × 25.000.

Fig. 54.

Polished and etched (30 sec.) oblique section of the siphonal funnel of one of the small adapical septa. Outer portion of the calcareous ring limiting inward the septal mother-of-pearl.

Parallel elongated elements (with their pseudoreplicas : black rods) appearing as needles or spindles when viewed on their sharp edges, are grouped in two bundles in which the individual crystals are involved longitudinally (upper group) and obliquely transversely (lower group) in the plane of polishing.

These bundles are probably the rounded calcareous bodies described and illustrated by APPELLÖF (1893 : p. 83, and Pl. XI, figs 2 and 4) in the inner calcareous layer (HÜLLE) of the siphonal funnel.

Direct print : 16.000.

PLATE XVI.

Nautilus pompilius LAMARCK.

Fig. 55.

Polished and etched (30 sec.) transverse, slightly oblique section of the ultimate septum, showing a thick lamella interposed between stratified lamellae composed of large tabular crystals. Comparison between this structure and that of the lamellae in the adapical septa (figs 50 and 51) suggests that the constitution of the last septum took place more slowly than that of the early septa. Debris of reticulated sheets are collapsed downwards on to the crystals of the thick lamella.

Reversed print : × 25.000.

Fig. 56.

Surface of fracture of the last adoral but three septum, showing eighteen superimposed broken lamellae in transverse section. Interlamellar reticulated sheets of conchiolin (horizontal white strings in the figure) alternate with the mineral lamellae. The white rectangular areas (on right side of the figure) are pseudoreplicas of fragments of aragonite crystals.

On the tenth lamella down from the top, a conchiolin bridge, separating two crystals of aragonite in this lamella, forms a right angle with the adjacent interlamellar sheets, above and below. The lace-like textures of the interlamellar reticulated sheets of conchiolin are visible as latticeworks protruding from the background and projecting shadows over the second, third, fourth and tenth mineral lamellae respectively.

Reversed print : × 19.000.

Fig. 57.

Conchiolin from decalcified septal mother-of-pearl collected from the concave side of the last but nine septum.

Preparation as described in fig. 39. See legend of fig. 59.

Reserved print : × 43.000.

Fig. 58.

Polished and etched (30 sec.) section of the siphonal funnel of one of the small adapical septa.

Brush-shaped arrangement (BROOKS, 1888 : bundles of faggots) of elongated girders of the calcareous sheath lining the inner organic membrane (« internal chitineous layer » : APPELLÖF, 1893; MUTVEI, 1956, disappeared in the present material) which surrounds the funnel opening. These girders, separated from the septal nacreous layer by the circular layer of bundles shown in fig. 54 (APPELLÖF's rounded calcareous bodies) are the calcareous needles or spicules described by BROOKS (1888) and by APPELLÖF (1893, p. 83-84, Pl. XI, figs 2 and 4 : Pfeilerchen) in the inner calcareous layer of the siphonal funnel.

Reversed print : × 10.000.

PLATE XVII.

Nautilus pompilius LAMARCK.

Fig. 59.

Conchiolin from decalcified septal mother-of-pearl collected from the middle portion of the penultimate septum.

Preparation as described in fig. 39 (see also fig. 57).

In the fragment of lace-like reticulated sheet here shown, the « nautiloid pattern » of nacreous conchiolin of the shell wall (fig. 39), is recognizable. However, the texture of the septal reticulated sheets is tighter, the trabeculae more slender, the openings smaller, sometimes rounded (see fig. 57). As on the sheets of the shell wall, numerous rounded tuberosities are bulging on the trabeculae.

Reversed print : × 43.000.

Fig. 60.

Posterior membrane coating the adapical convex side of a septum in the anterior part of the phragmocone. Material from a living specimen presumably immersed in alcohol immediately after capture, supplied by Dr. C. TEICHERT. The preparation is a thin fragment detached from the membrane, deposited on formvar films and shadow cast at a low angle (15°).

The membrane consists essentially of microfibrillar layers in which the fibrils, either solitary or associated in bundles and in fibers, form an unoriented felting. Identical structures were also observed in the replicas of the membrane remained undisturbed in its original position, especially in the adapical camerae (see figs 43 and 44). Irregularly rounded nodules are scattered among the fibrils, which frequently anchor to them in a beam-like fashion.

Reversed print : × 43.000.

PLATE XVIII.

Nautilus pompilius LAMARCK.

Figs 61, 62 and 63.

Posterior membrane coating the convex side of a septum (continued, see legend of fig. 60).

In figs 61 and 62, the relationships between nodules and fibrils are shown after loosening and moderate disintegration of the felting by ultrasonic waves. In fig. 63, nodules are scattered on sturdy fibers crossed at random by thin fibrils.

Reversed prints. Fig. 61 : × 16.000; fig. 62 : × 34.000; fig. 63 : × 42.000.

PLATE XIX.

Nautilus pompilius LAMARCK.

Fig. 64.

Polished and etched (30 sec.) transverse section of the last septum, involving the edge of the convex side and the posterior membrane (above) preserved in its topography by the embedding substance.

The organic structures revealed by the etching process appear folded or collapsed on to the mineral background. From top to bottom :

1. torn and folded shreds from the felting of the posterior membrane;

2. straight line of demarcation between posterior membrane and septal mother-of-pearl;

3. shreds of an amorphous veil collapsed downwards;

4. the brick wall configuration of the septal nacreous substance, in which conchiolin membranes running between the stratified lamellae and transverse bridges of organic substance separating the aragonite crystals in each lamella, are shown. In this preparation, the organic components of the posterior membrane and those of the septal mother-of-pearl appear merely juxtaposed without visible anatomical connection. The fragments of amorphous veil collapsed on to the nacreous substance at the line of demarcation represent probably a metallic replica of the interspace between the posterior membrane and the septal mother-of-pearl.

Direct print : × 25.000.

Figs 65 and 67.

Polished and etched (60 sec.) transverse sections of the phragmocone. Structure of the sutural cements interposed between the mural part of the penultimate septum and the adjacent shell wall (textfigs 4 and 5 : SC).

Fig. 65 shows in succession, from bottom to top :

1. the nacreous lamellar stratification (below left. Textfigs 4, 5 and 6 : SW, zone 1);

2. the helle Schicht, with its columnar structure and the internal subdivisions of its elongated crystals (textfigs 4 and 6 : H S, zone 2). In this preparation, the nacreous layers grown over the helle Schicht after the muscles moved forward adorally, were too irregular in structure to be distinguished from the components of the helle Schicht;

3. a light and a dark parallel strands of uncalcified organic substance (textfigs 4, 5 and 6 : zone 3);

4. at the upper right corner of the figure, the beginning of a palisade of elongated crystals (textfigs 4, 5 and 6 : zone 4).

Direct print : × 16.000.

Fig. 67 shows details of structure of a broad strand of amorphous substance interposed between two palisades (textfigs 4, 5 and 6 : zone 3). Roughly rectangular bulging bodies, aligned in three rows, are separated from one another by longitudinal and transverse furrows. These bodies, of undetermined nature and structure, appear thinly striated transversely and composed of numerous superimposed extremely thin sheets of substance.

A palisade of elongated elements (textfigs 4, 5 and 6 : zone 4) is shown at the upper right corner of the figure. In other preparations of the same region (not shown), substantial systems of stratified fibrillar layers were embedded in the amorphous material.

Direct print : × 14.500.

Fig. 66.

Polished and etched (100 sec.) transverse section of another region of intersection of the shell wall and of a septum.

From left to right :

1. a strand of organic amorphous substance (textfigs 4, 5 and 6 : zone 3) in which the bulging outlines of embedded crystals are visible;

2. a palisade of parallel elongated, imbricated tablets, blades or bars, viewed on their sharp edges in the form of girders, with their needle-like pseudoreplicas (in black) (textfigs 4 and 6 : zone 4);

3. two parallel strands of amorphous substance (textfigs 4 and 6 : zone 3). Small hillocks (microcrystals) protrude on the surface of the strand in the centre of the figure. The surface of the dark strand (right), on which the outlines of a small rounded hexagonal crystal are visible, is crossed by faint traces of parallel ripples. Numerous undulating linear shadows appearing on its slopes towards the adjacent strand, suggest a thinly stratified organization of the substance composing this strand (compare with fig. 67). At the right upper corner of the figure, the beginning of a palisade of elongated elements is visible.

Direct print : × 14.500.

PLATE XX.

Nautilus pompilius LAMARCK.

Figs 68, 69 and 70.

Polished and etched transverse sections (60 sec.) of the phragmocone.

Structure of the sutural substances sandwiched between the mural part of the penultimate septum and the adjacent shell wall. (See figs 65 and 67, and textfig. 6).

Fig. 68 : The edges of imbricated, elongated tablets involved obliquely in the plane of polishing and arranged in palisades, appear as spindle-shaped girders on the polished surface. A portion of an adjacent strand of amorphous substance is visible at the right part of the figure (textfig. 6 : zone 4, bottom right).

Figs 69 and 70 : Portions of the yellowish calcareous concretions which overlap the milk-white sutural substances (cements) towards the cameral cavity (textfig. 4 : MEI, CI, CR, SEI and zone 5). These infillings are characterized by a great variety of shapes and of arrangements of their mineral components. The dense concentric (fig. 69) or undulating (fig. 70) stratification confers to these substances the appearance of polished chalcedony or agate.

Direct prints : × 25.000.

PLATE XXI.

Nautilus pompilius LAMARCK (fig. 71).

Pseudorthoceras knoxense MC CHESNEY.

(Lower Middle Pennsylvanian, Buckhorn asphalt, Sulfur, Oklahoma.) (Figs 72 and 73.)

Fig. 71.

Polished and etched (3 min.) transverse section of the region of intersection of the shell wall and of a septum in the middle part of the phragmocone.

The surface of the area here shown (textfigs 4 and 6 : zone 5) appears subdivided into roughly rectangular fields surrounded by thick white cords of substance. These fields stacked upon one another in several parallel lines are probably transverse or oblique sections of elongated sharp-edged tablets or blades. The white cords are possibly in part metallized replicas of microcracks induced by the heavy etching and more probably shreds of organic substance, particularly substantial in this region, as shown in plate 24, figs 78 and 79.

Reversed print : × 30.000.

Fig. 72.

Polished and etched (15 sec.) sagittal section of the shell. Hard calcified portion of the cameral deposits.

Parallel elongated tablets and blades viewed on their edges, grouped in about twelve bundles variously oriented. Identical elements, shown in several figures above (figs 14, 15-19, 21-24, 26, 54 and 68) characterize the structure of the porcellaneous substance in the *Nautilus* shell.

Direct print : × 14.500.

Fig. 73.

Pseudorthoceras knoxense MC CHESNEY.

Polished unetched sagittal section of the shell. Calcified marble-like portion of the cameral deposits. Parallel elongated crystals packed without visible interposition of organic substance are shown. These structures reveal possibly a local process of recrystallization of calcium carbonate. The crystallographic nature of the crystals composing this area has not been determined. However, X-ray diffraction analysis of samples collected in this region, performed by Mr. J. GRANDJEAN (Centre National de Recherches Métallurgiques) indicates that this material consists chiefly of aragonite.

Reversed print : × 9.000.

PLATE XXII.

Nautilus macromphalus Sowerby (fig. 74).

Pseudorthoceras knoxense Mc Chesney (fig. 75).

Fig. 74.

Polished and etched (25 sec.) transverse section of the phragmocone in the region of intersection of the shell wall and of one of the adoral septa.

The figure shows a portion of a broad palisade (textfigs 4 and 6 : zone 4) composed of parallel, imbricated, elongated tablets or blades which characterize the structure of the sutural cements. Inside the palisade here shown, the elongated elements appear assembled in bundles or pillars (see fig. 21).

Reversed print : × 22.000.

Fig. 75.

Polished and etched (2 min.) sagittal section of the shell. Partially calcified portion of the cameral deposits.

Parallel imbricated, elongated elements, similar in their shape to the elongated porcellaneous tablets, blades or bars shown in fig. 74 and here viewed on their edges, alternate with shreds of organic substance.

Reversed print : × 22.000.

PLATE XXIII.

Pseudorthoceras knoxense Mc Chesney.

Figs 76 and 77.

Polished unetched transverse sections of the shell. Partially calcified portions of the cameral deposits.

In these preparations, large differences in hardness of the microconstituents resulted in elimination by the abrasives used for polishing of the soft intercrystallinic organic substances, except for small fragments (f.i. shred in the centre of fig. 77) and in revealing the harder mineral components. These mineral structures consist of parallel elongated, spindle-shaped, finger-like crystals, grouped in about 19 bundles in the field shown in fig. 76. Orientation of the bundles varies greatly, and their crystallinic components appear disposed at various angles to the crystals of the neighbouring bundles. Elongated tablets and blades, identical to those characterizing the porcellaneous substance in *Nautilus,* were also detected in the present material. The disposition in bundles here shown resembles that described above in the outer and middle portions of the porcellaneous substance of the *Nautilus* shell.

Reversed prints. Fig. 76 : × 16.000; fig. 77 : × 25.000.

PLATE XXIV.

Nautilus pompilius Lamarck (figs 78, 79, 81, 82).

Nautilus macromphalus Sowerby (fig. 80).

Figs 78, 79, 82.

Organic residues from the decalcified material of the sutural infillings, collected at the intersection of the shell wall and of the septa, and dissected from the adjacent shell layers.

These organic residues consist of heterogeneous structures, among which thin veils (fig. 78), fibrils (fig. 79) and fibers (fig. 82). Fibrils and veils are involved in the constitution of the organic sheaths which wrap the elongated mineral elements of the sutural infillings as the identical crystals in the outer porcellaneous layer of the shell wall. On the other hand, the sturdy fibers (fig. 82) might be parts of the posterior membrane which intermingles, according to APPELLÖF (1893), with the calcareous deposits at the angles of intersection.

Direct prints : × 31.000.

Fig. 80.

Nacreous layer of the shell wall, slightly polished tangentially to the inner shell surface and etched with sequestrene (10 min.)

The outlines of two parallel hexagonal crystals dissolved by the etchant, with their a-axis running obliquely from the lower right to the upper left sides of the figure, are shown superimposed on the nacreous reticulated sheets on which these crystals had developed by epitaxial growth.

The a-axis of these crystals coincides with the direction of several underlying trabeculae. Such a relation does not appear clearly in the centre of the figure.

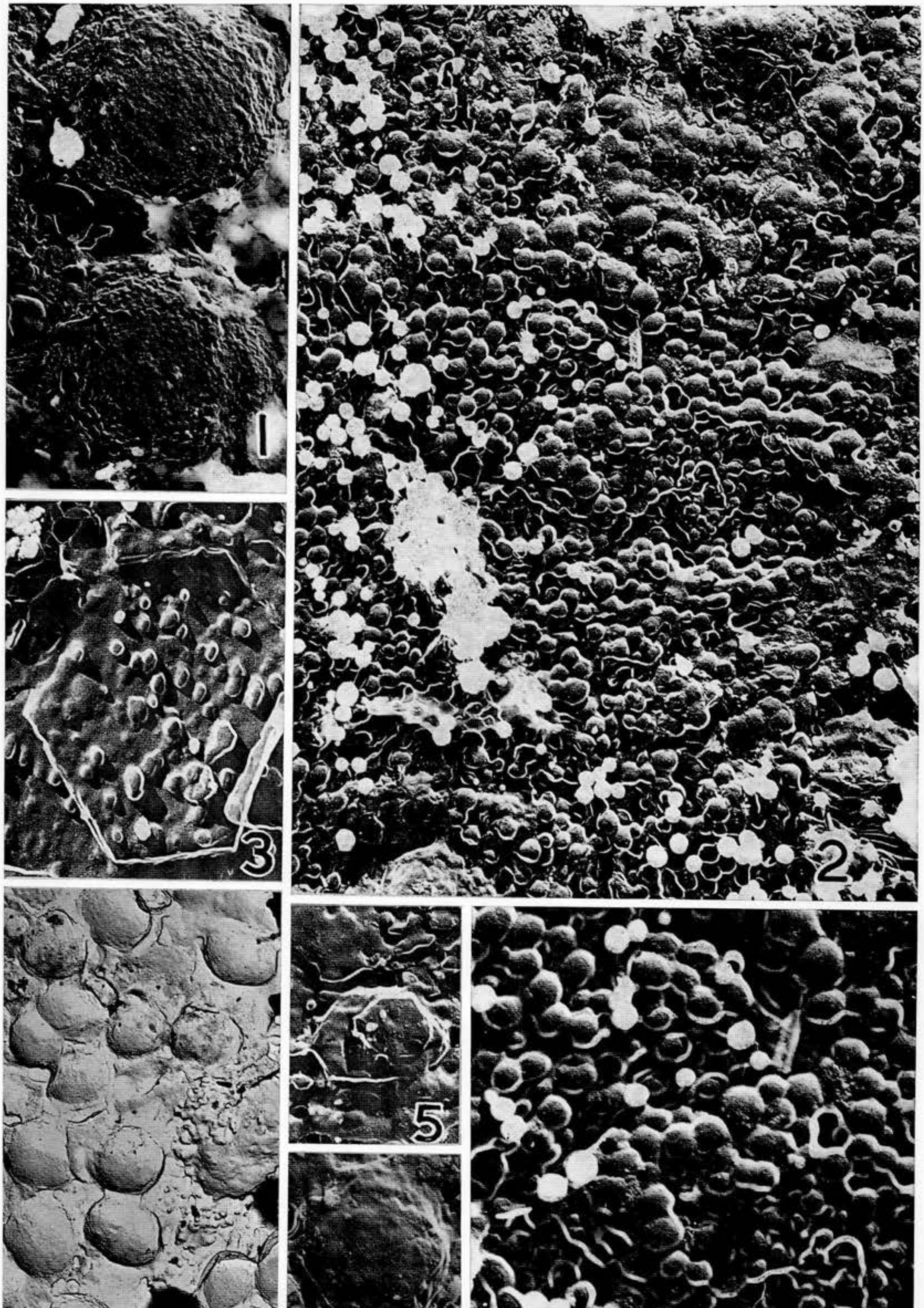
Reversed print : × 30.000.

Fig. 81.

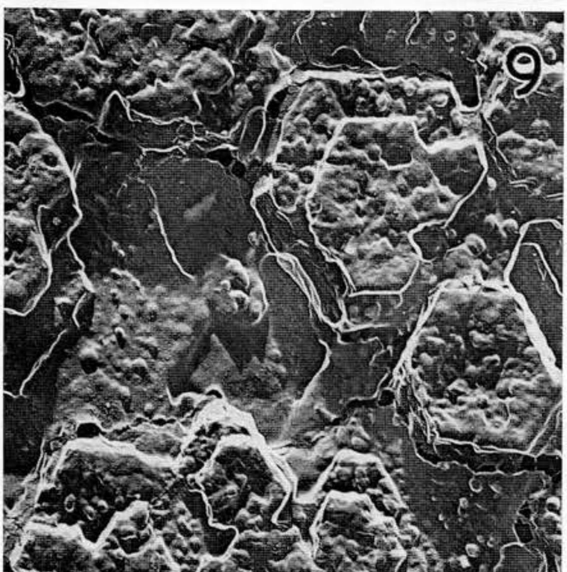
Concave adoral surface of the last but five septum. Portion of a large hexagonal tabular nacreous crystal.

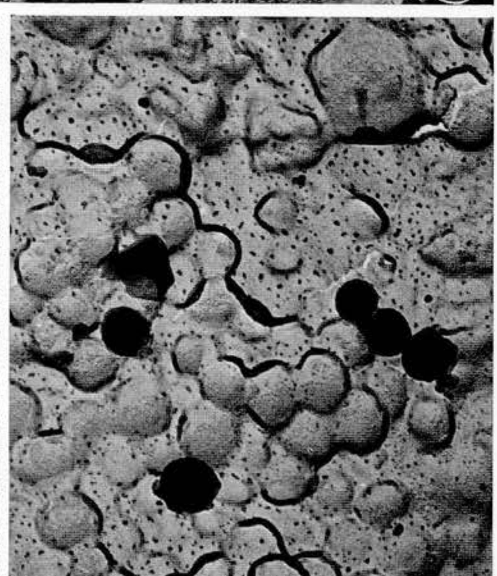
The a-axis of this crystal, disposed vertically in the figure, coincides with the predominant direction of the underlying trabeculae of the reticulated sheets of conchiolin.

Reversed print : × 30.000.



CH. GREGOIRE. — On submicroscopic structure of the Nautilus shell.





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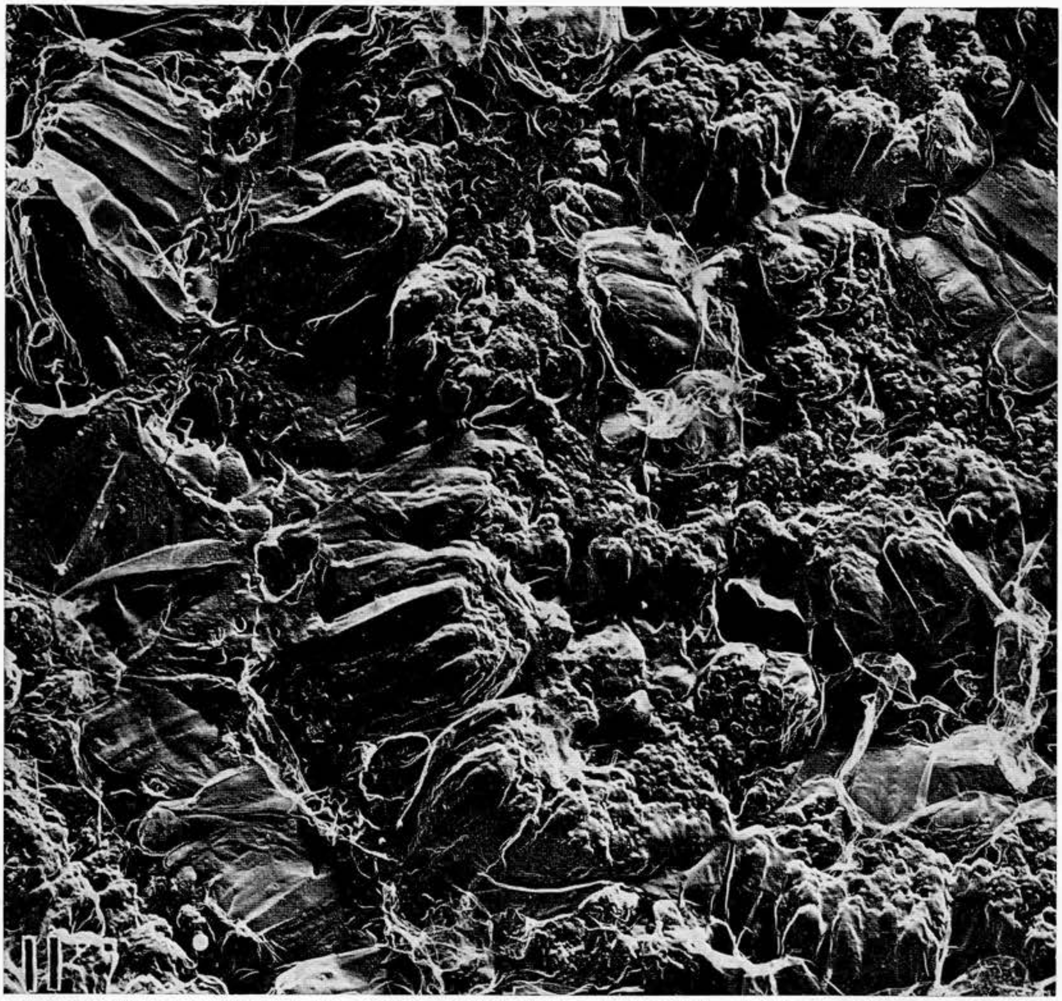

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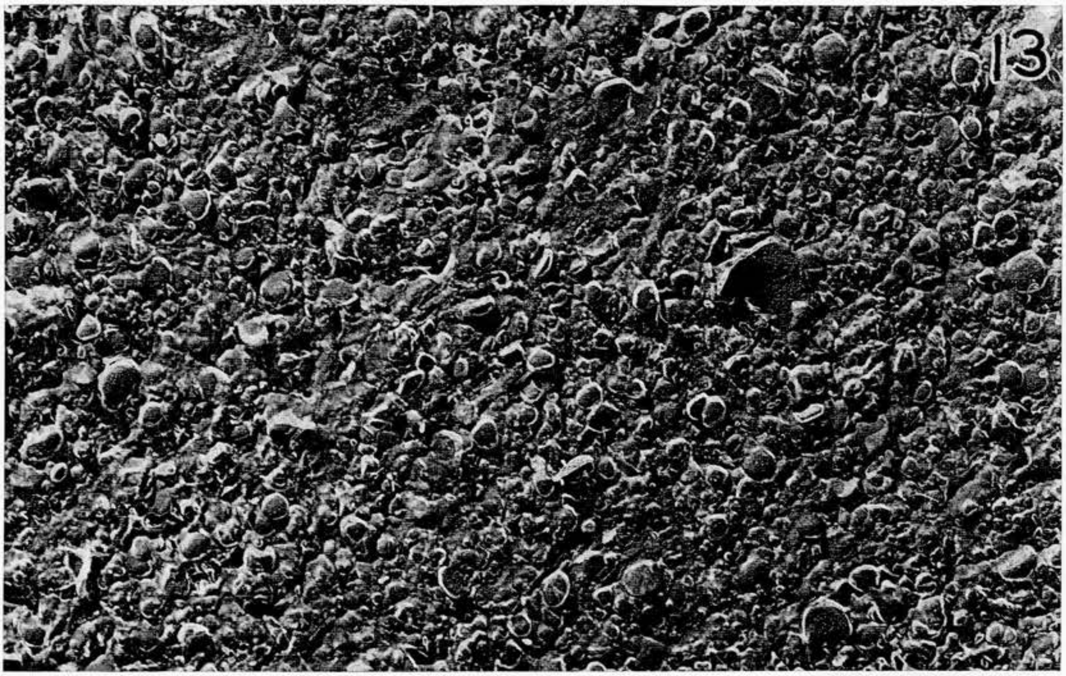

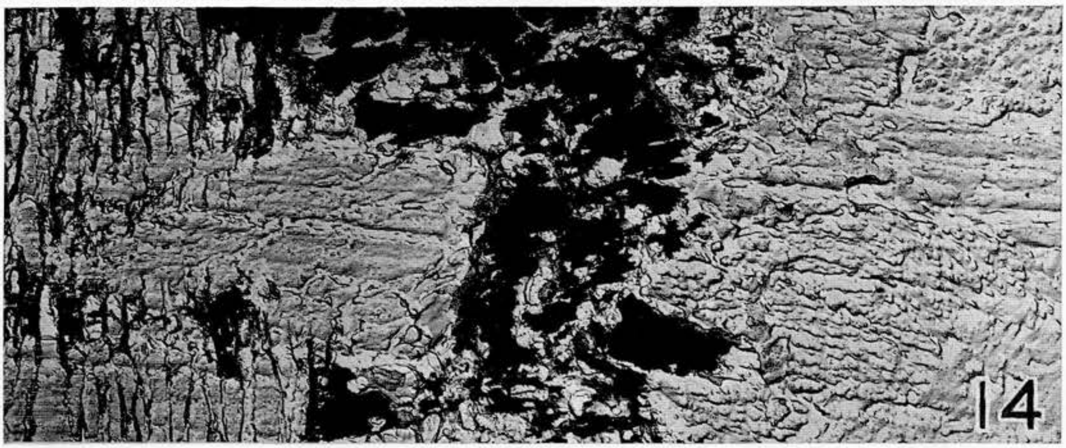

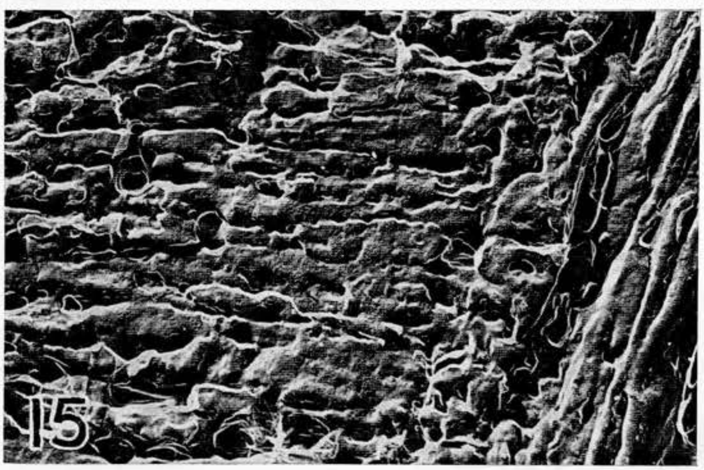

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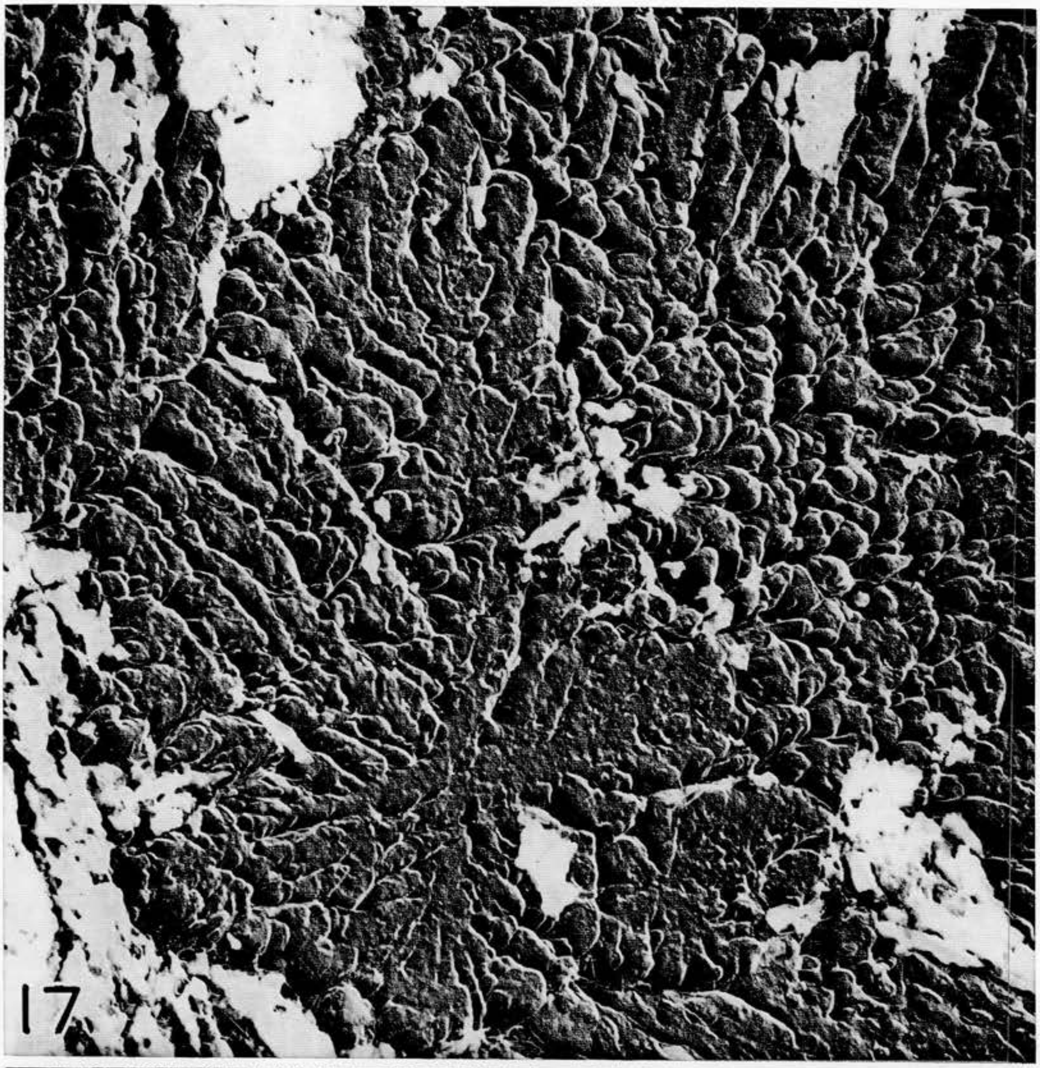

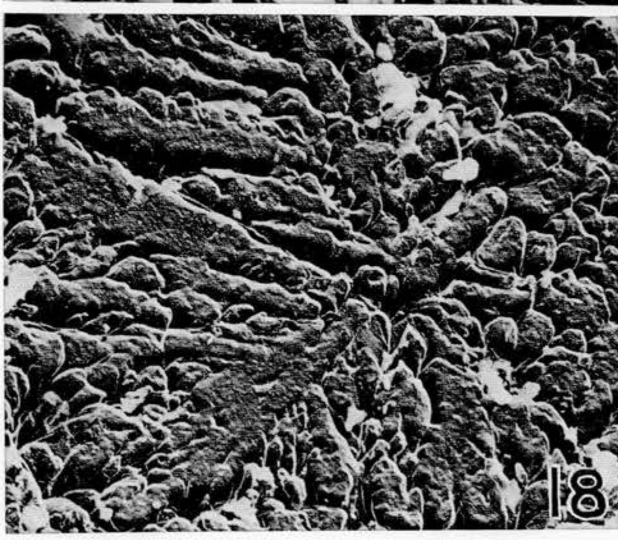

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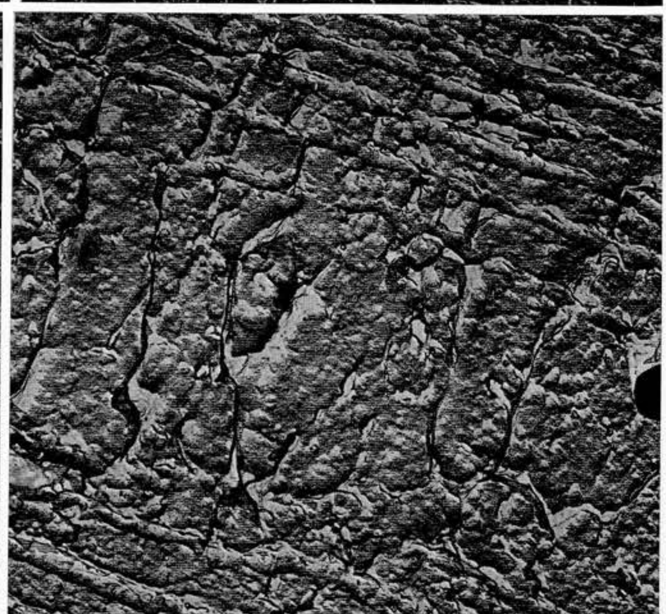

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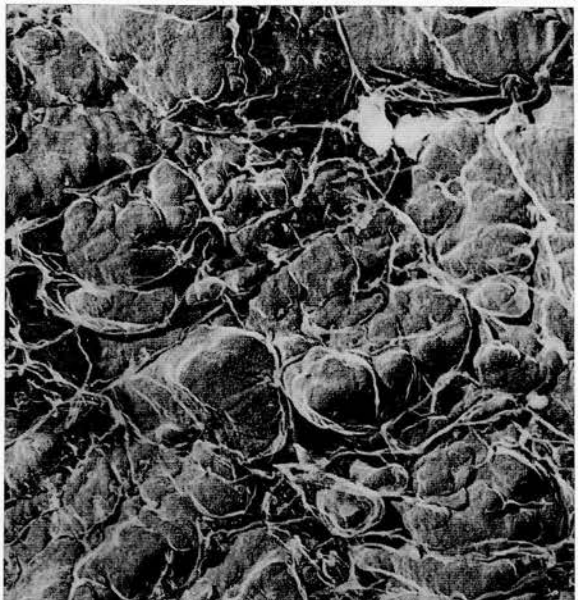

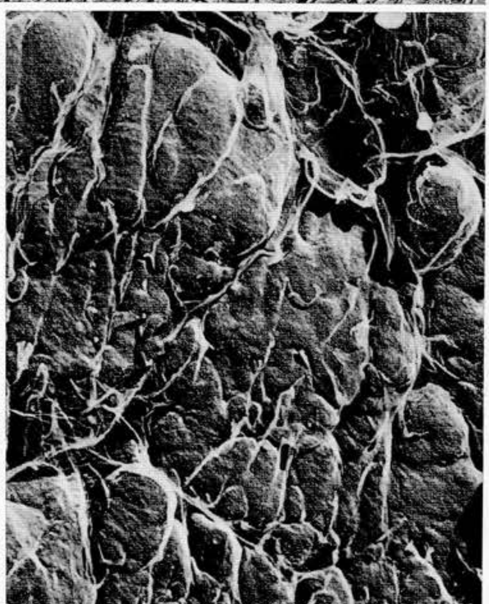

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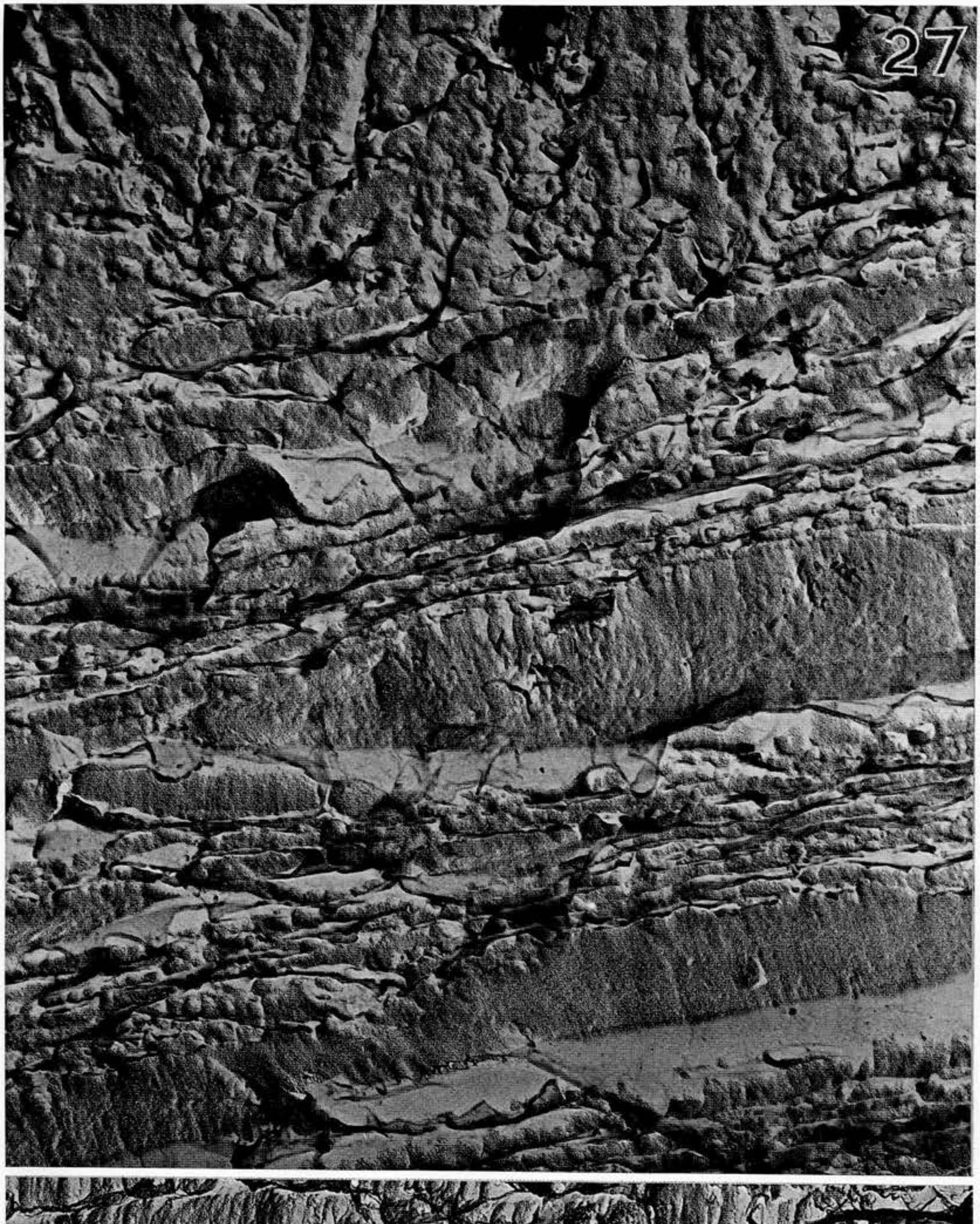

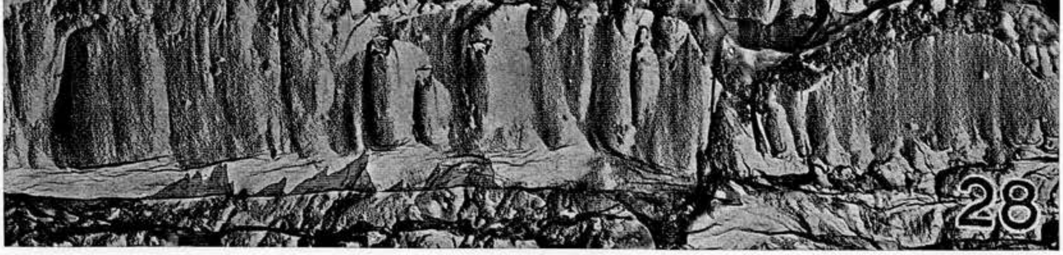

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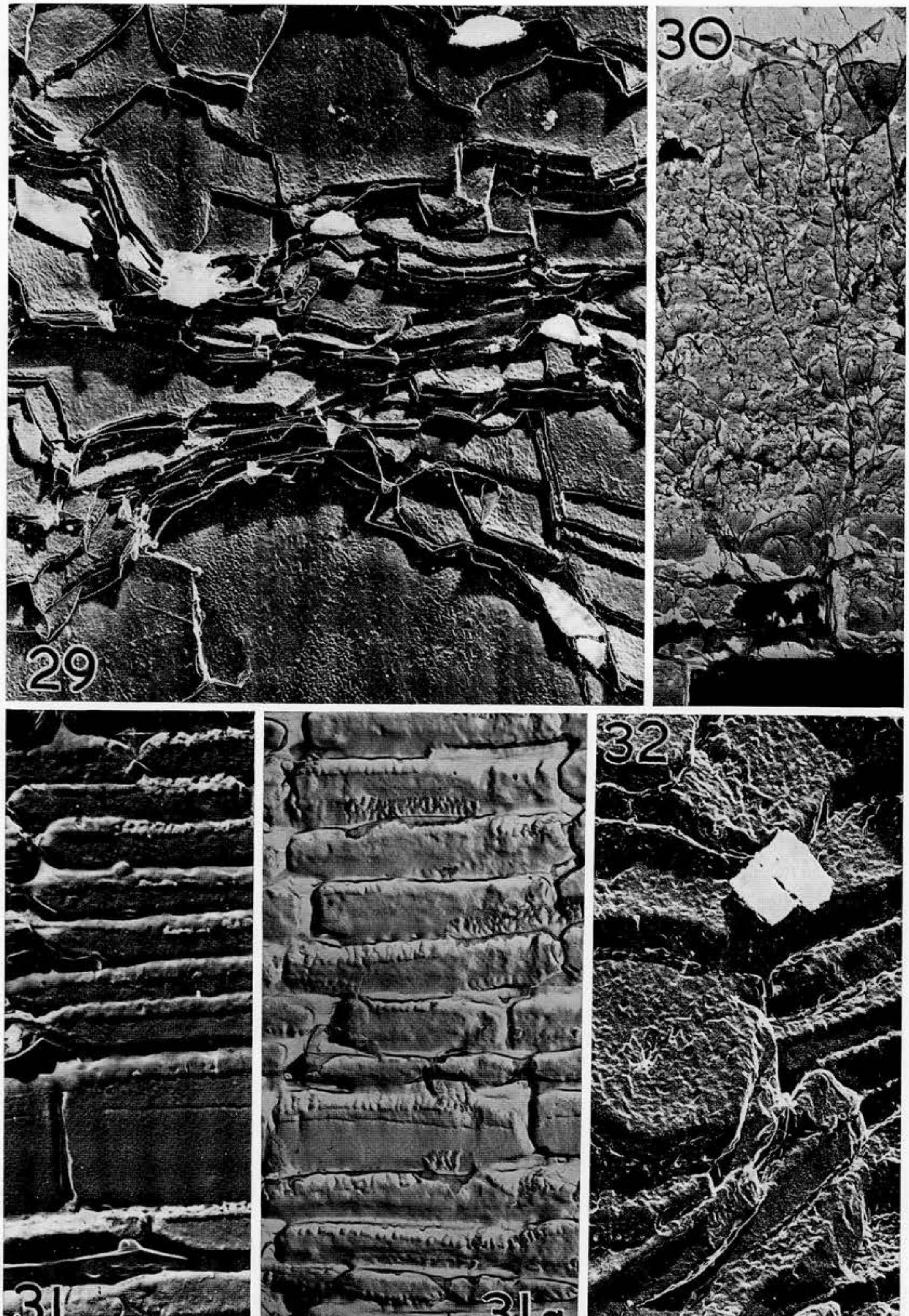

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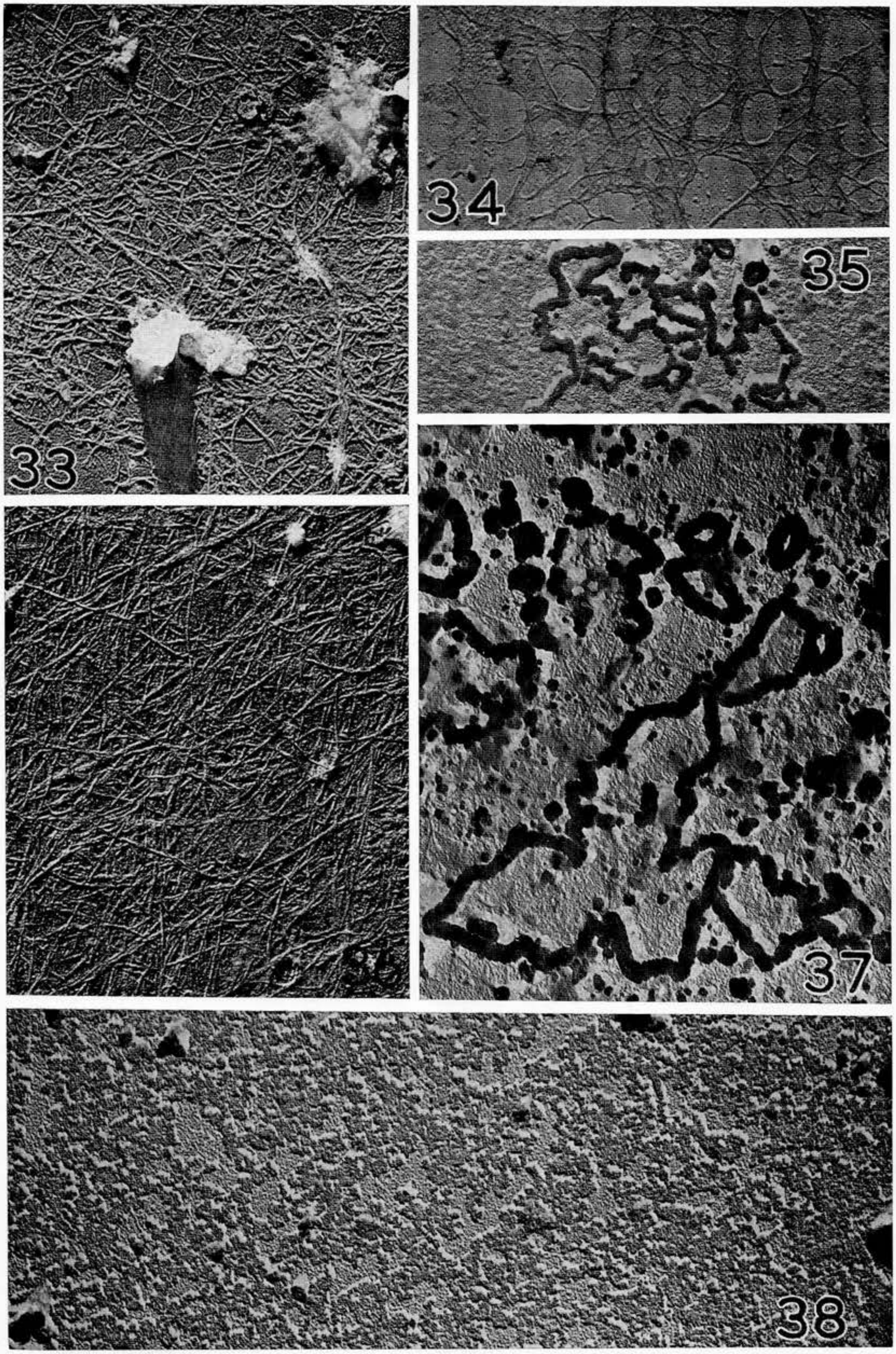

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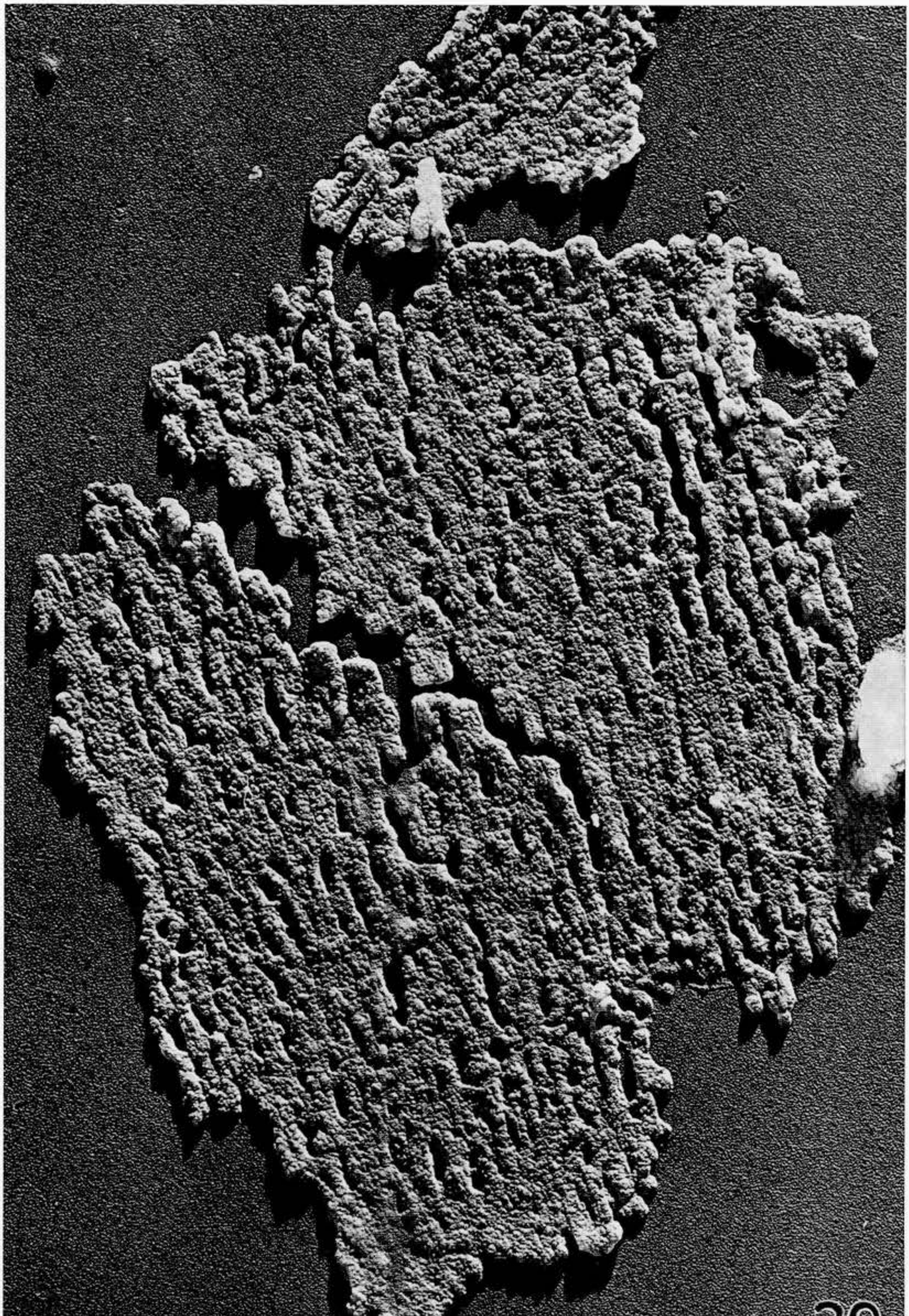

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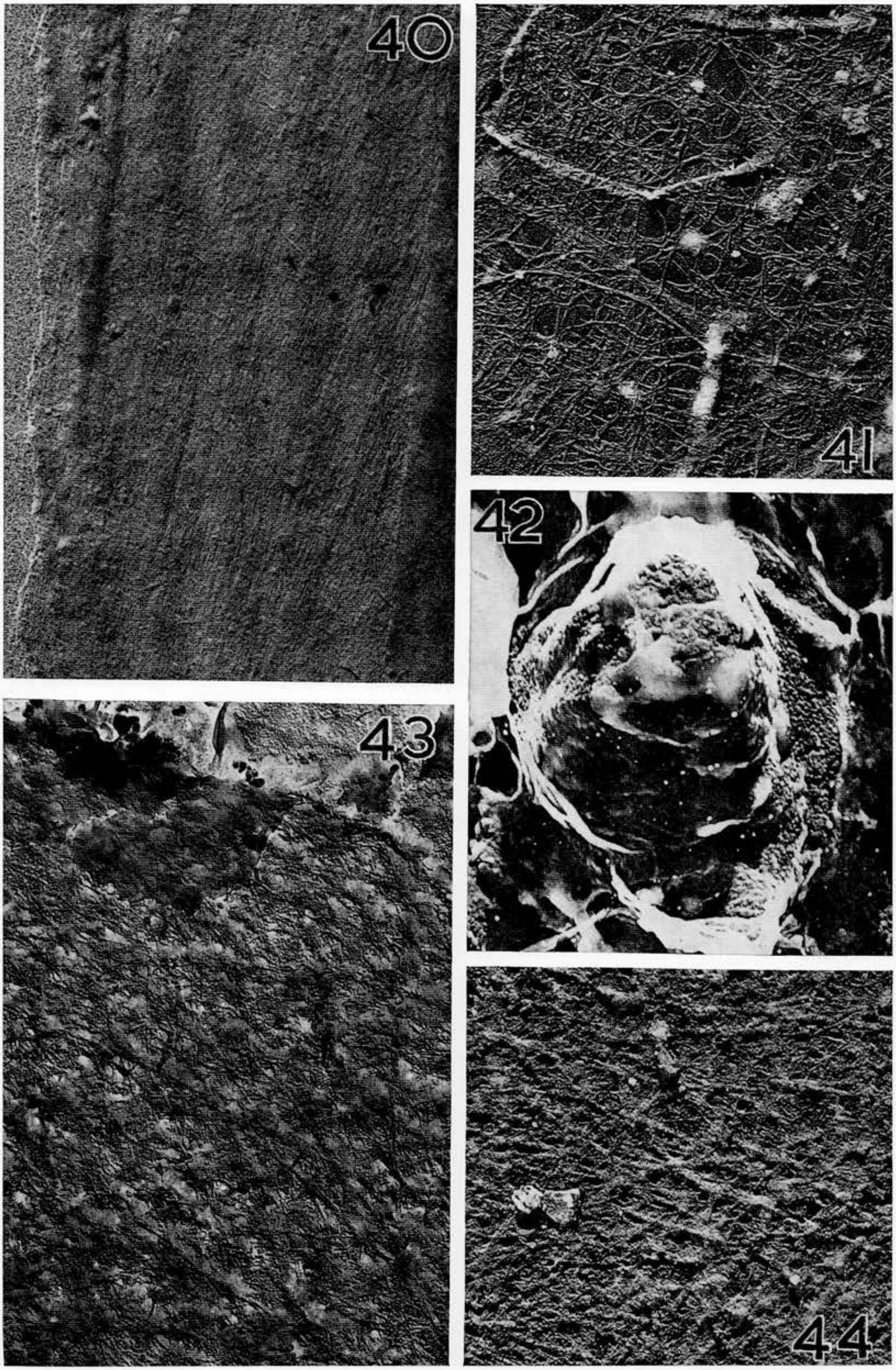

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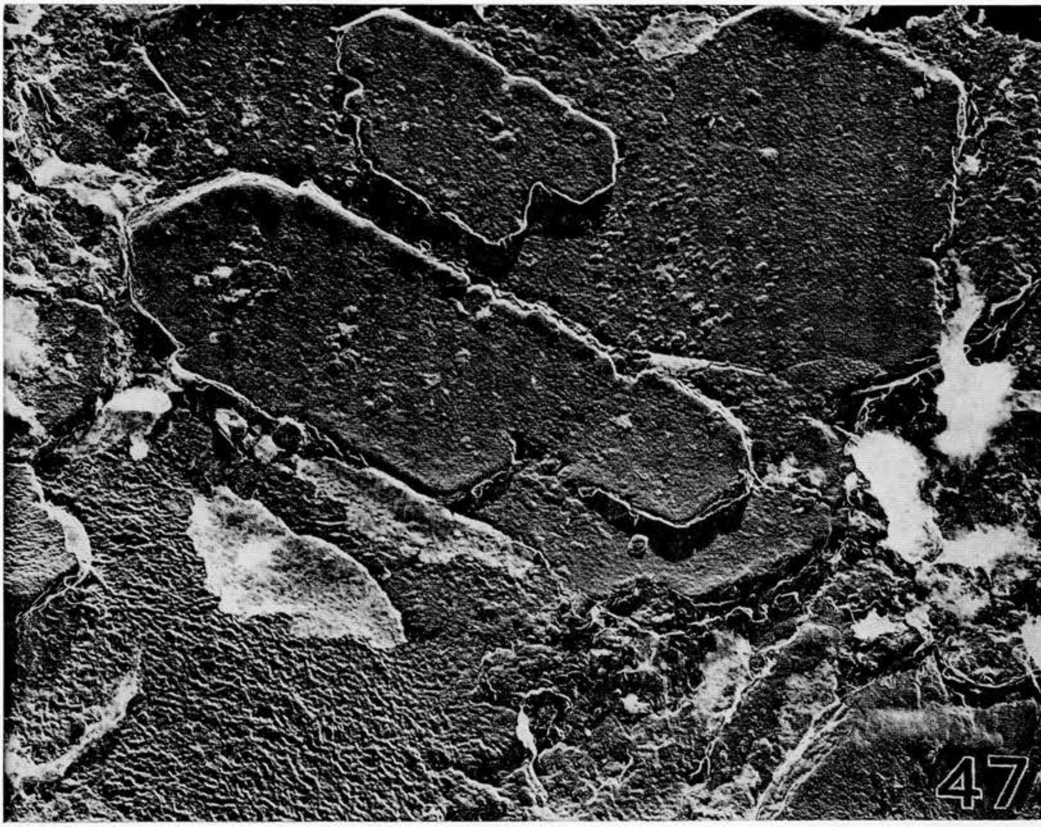

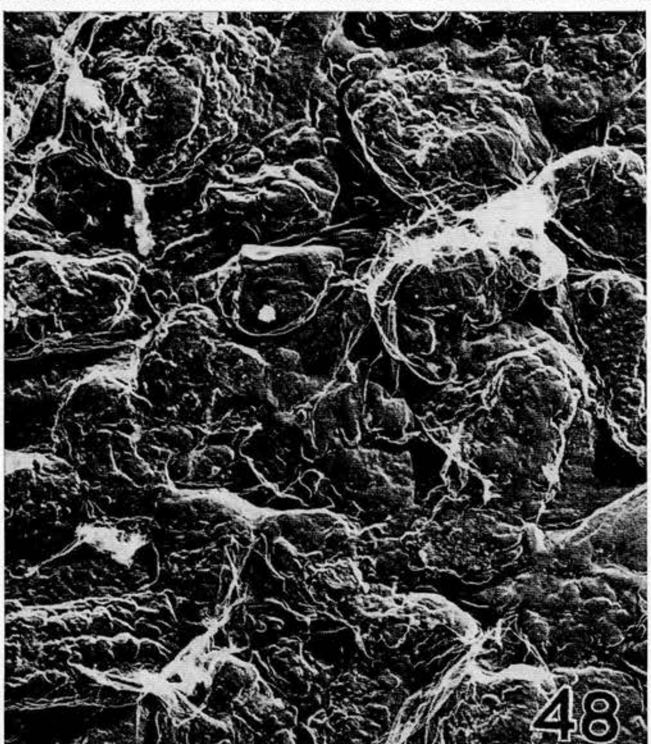

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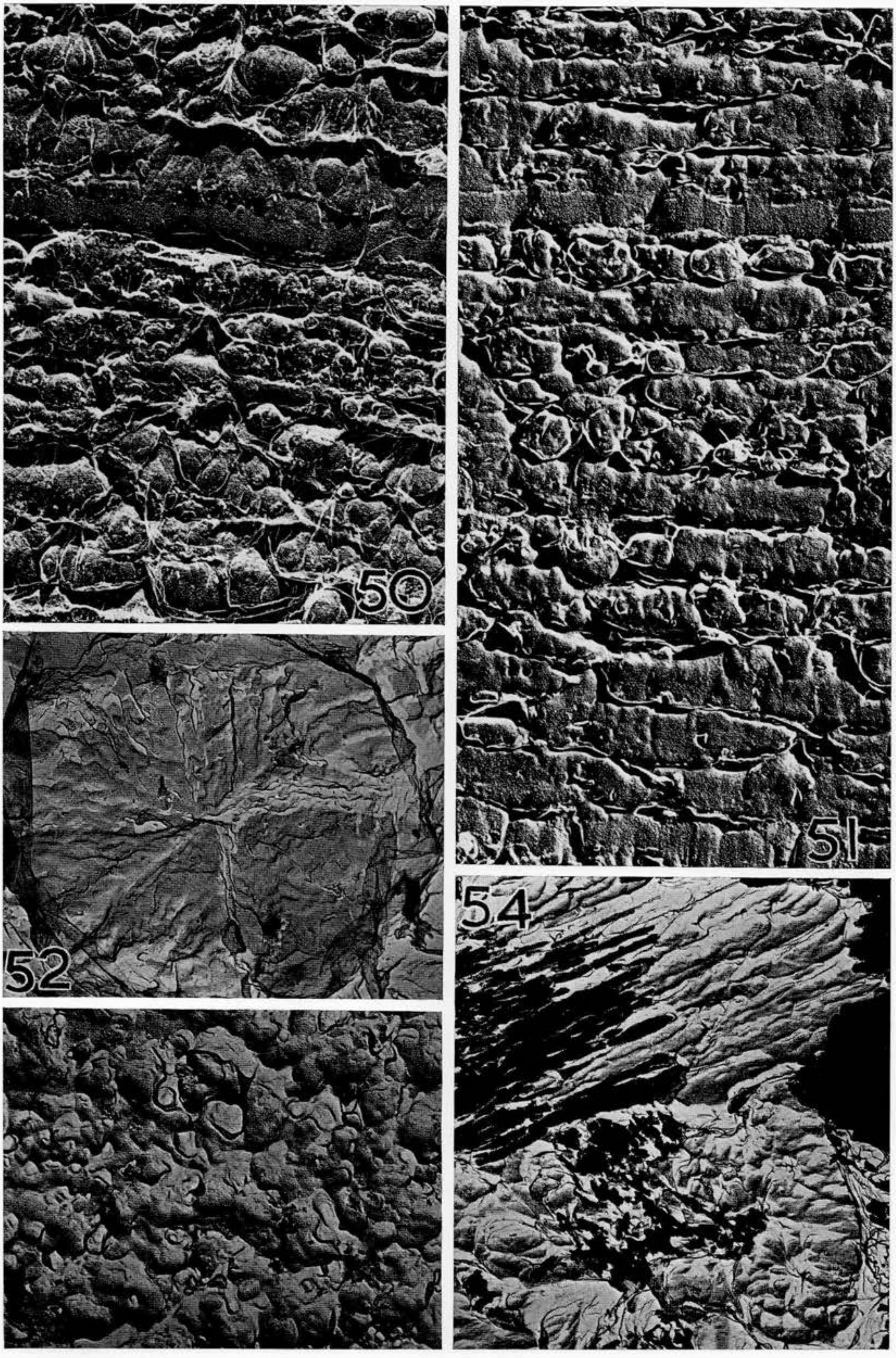

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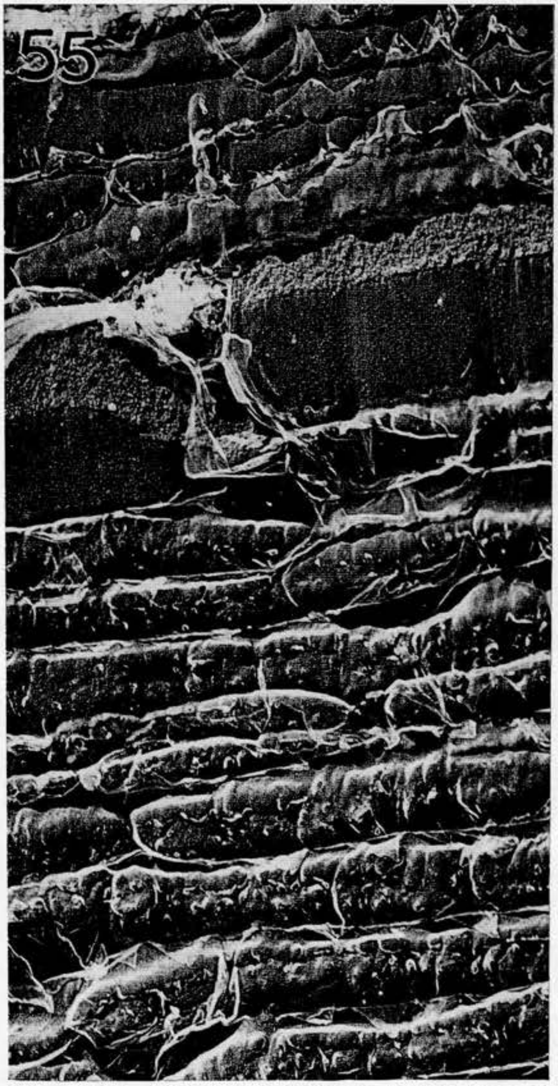

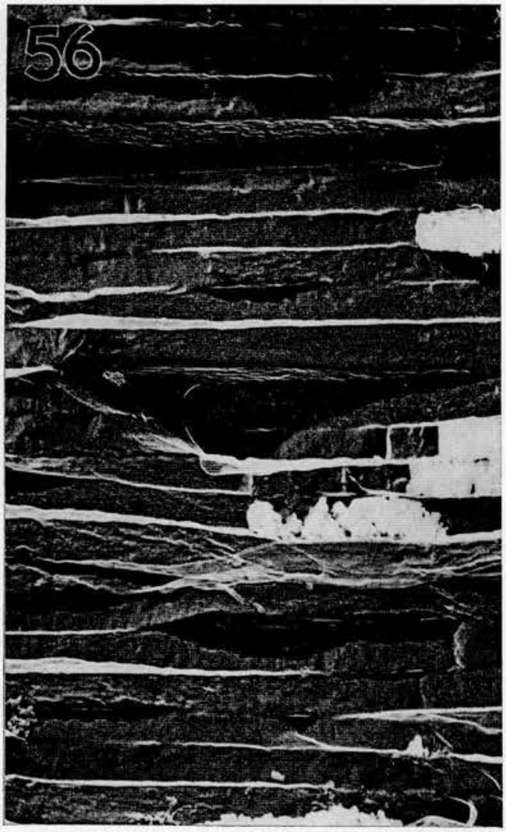

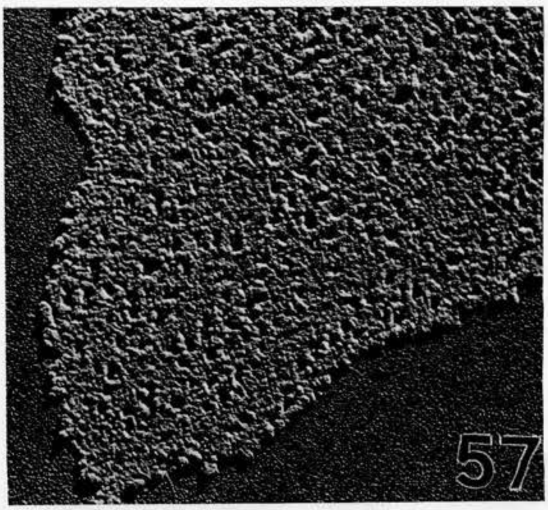

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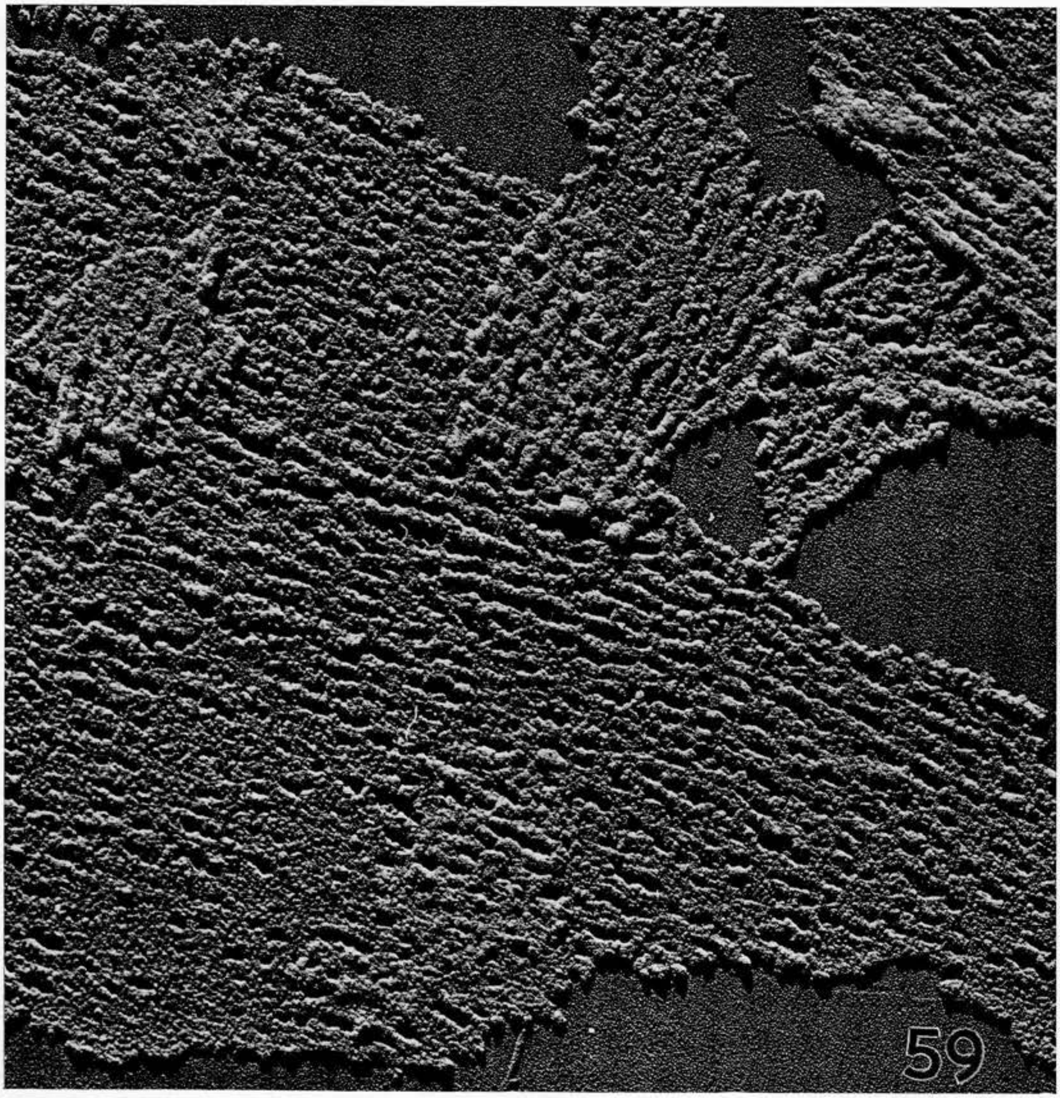

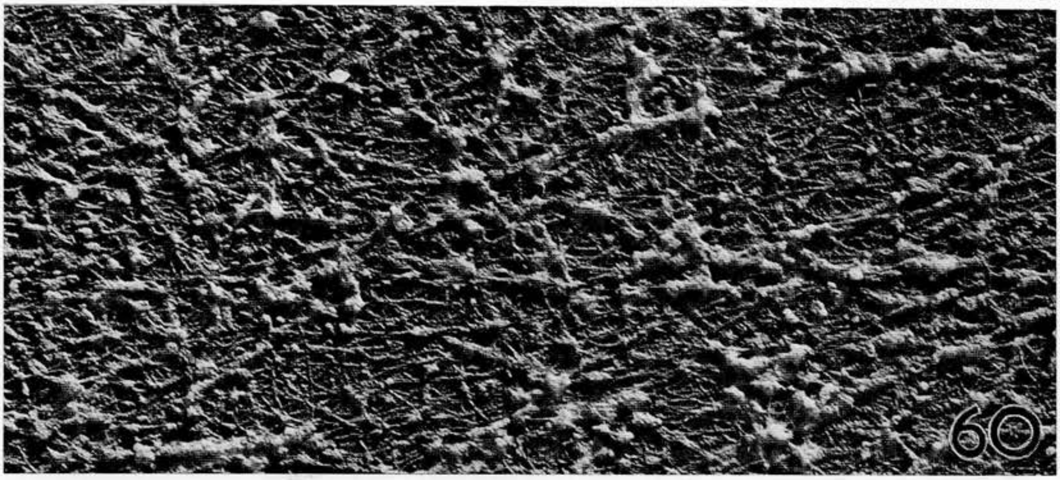

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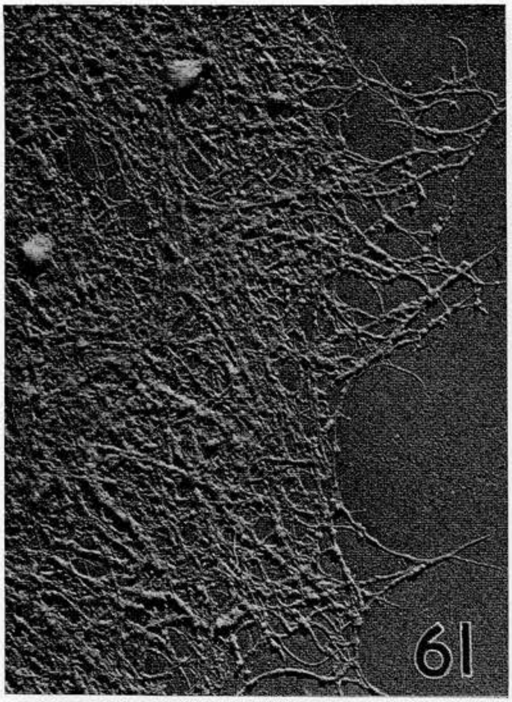

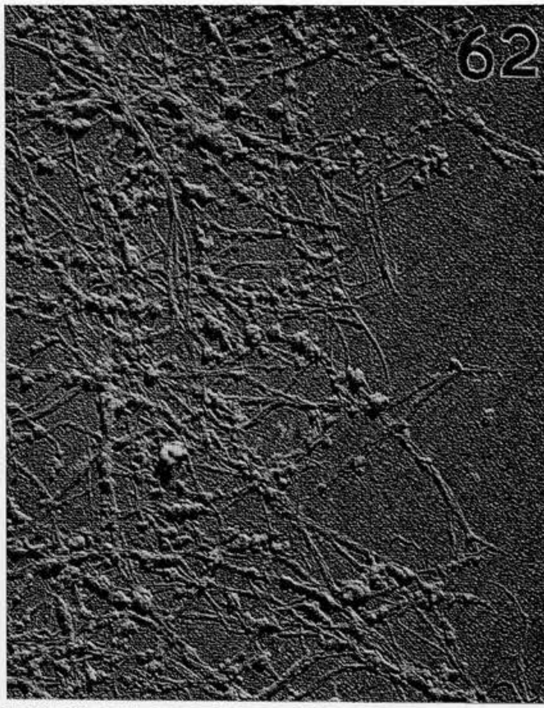

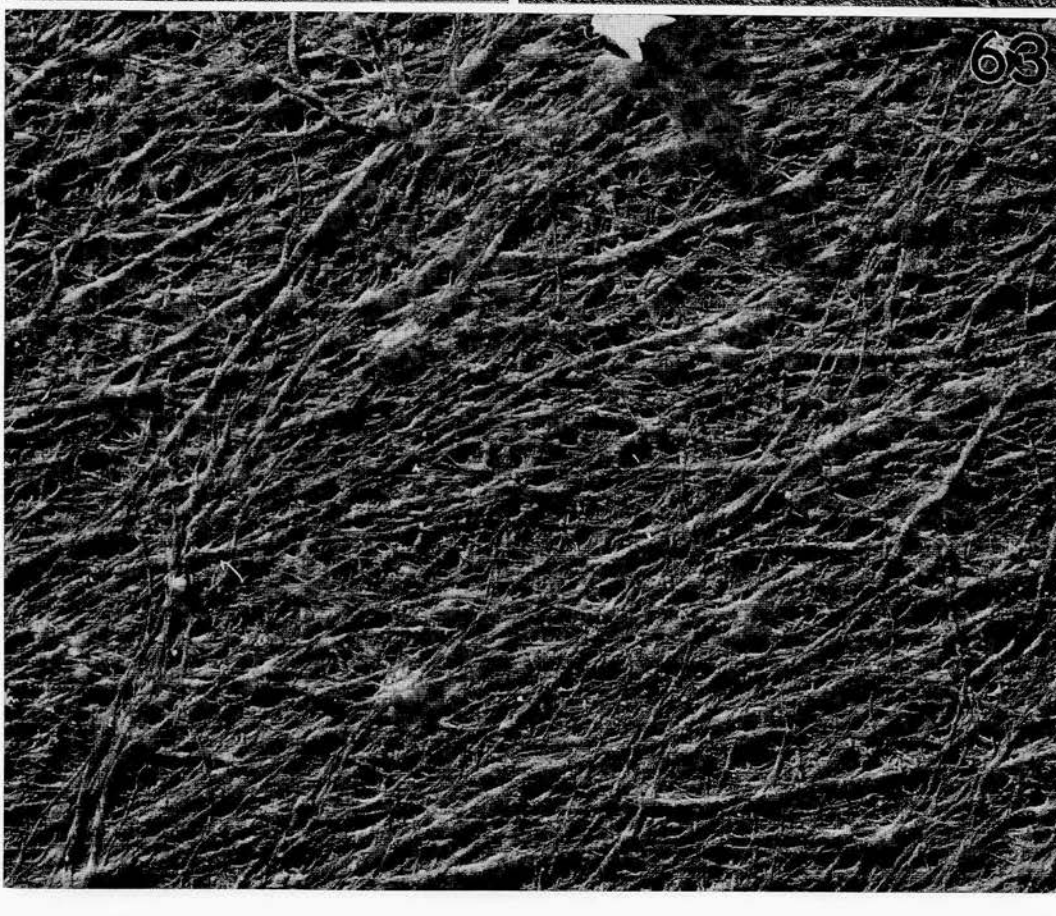

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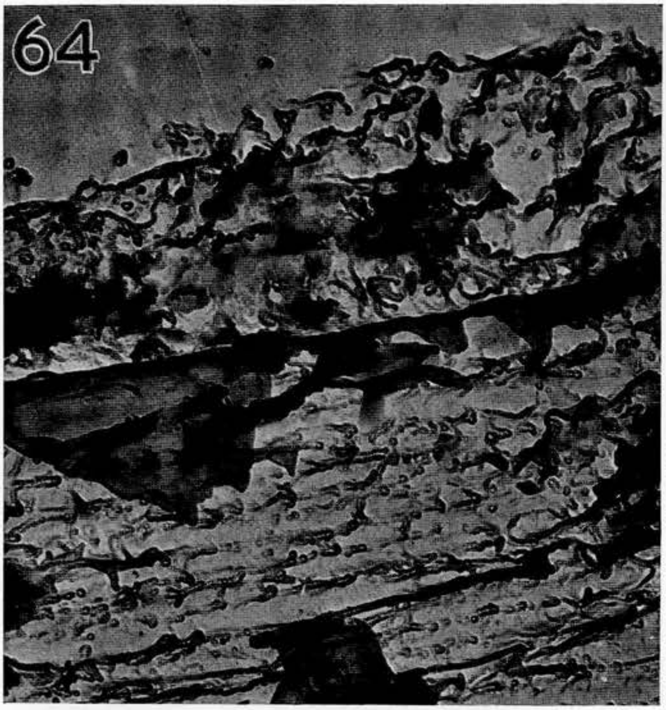

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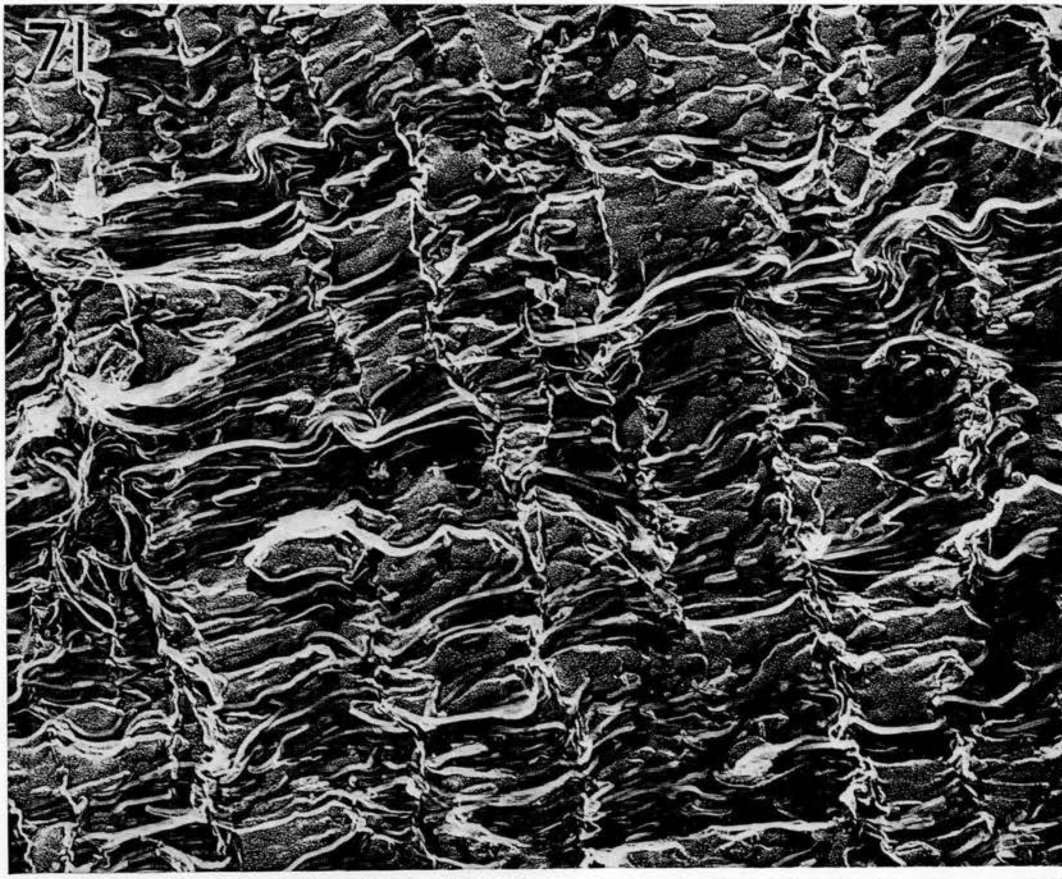

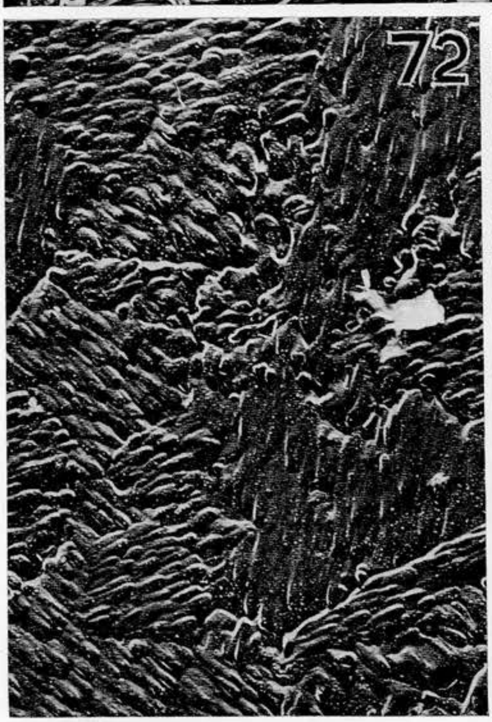

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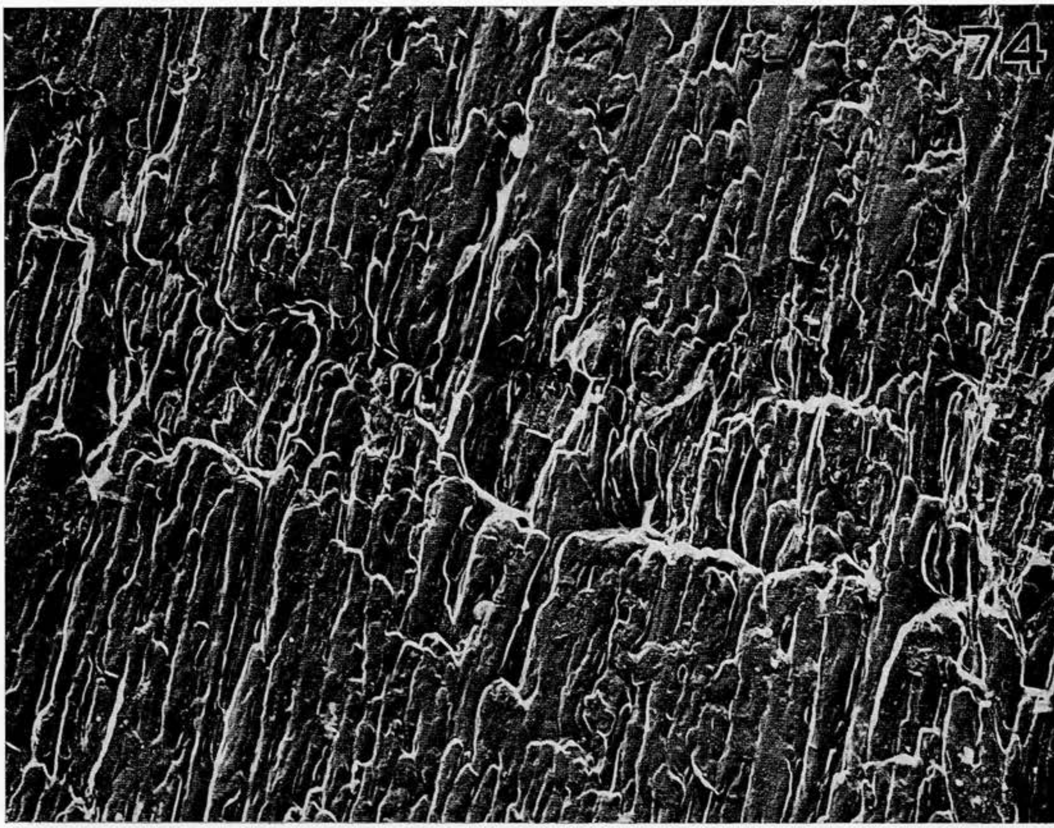
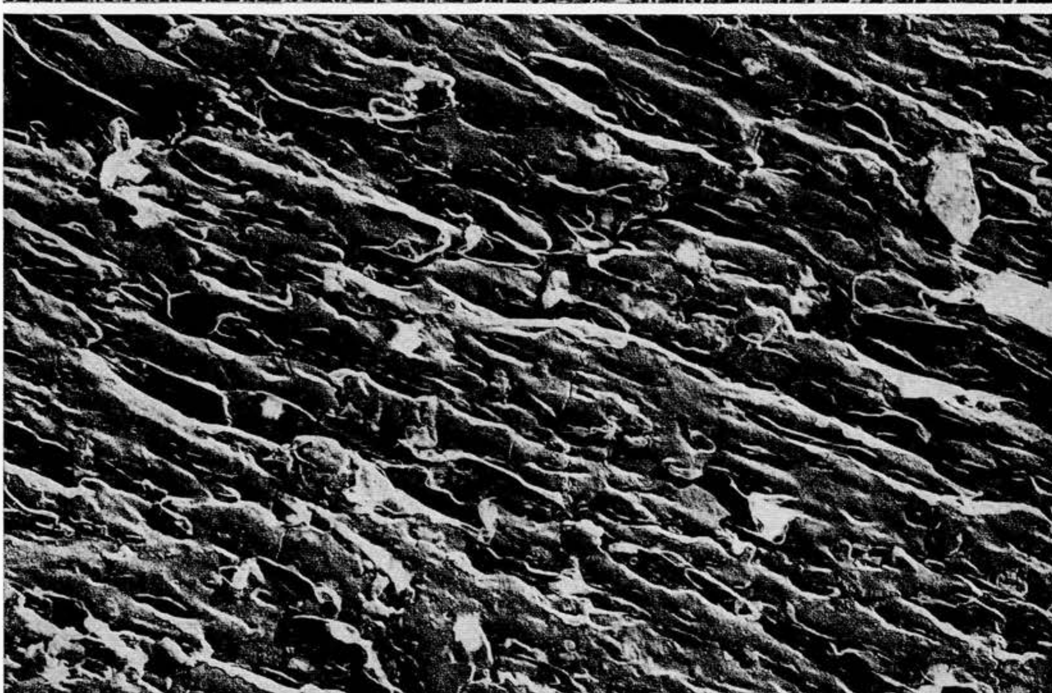
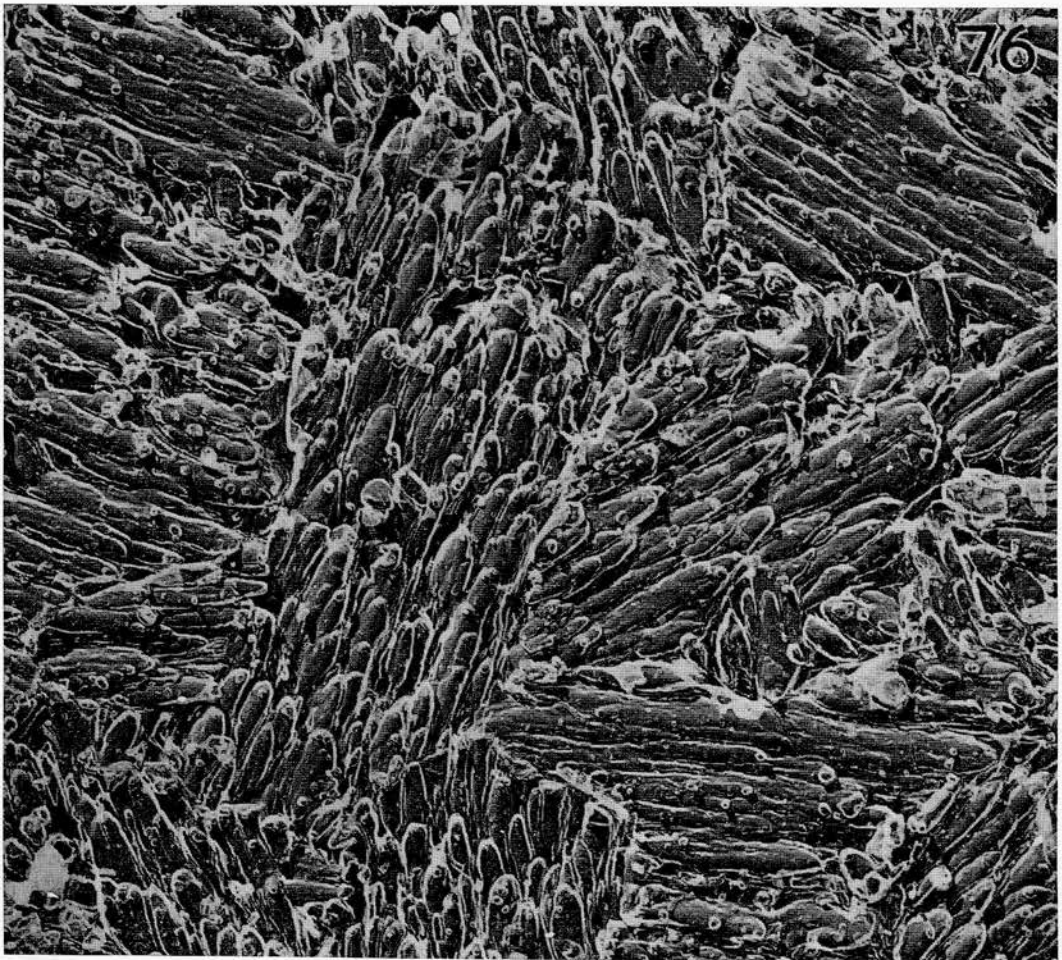
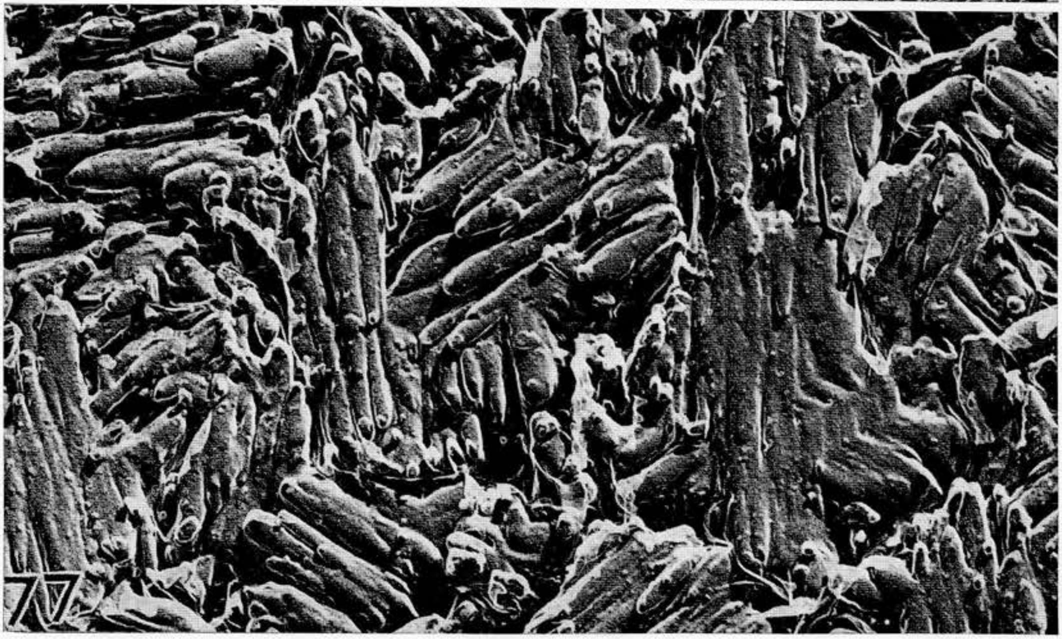




CH. GREGOIRE. — On submicroscopic structure of the Nautilus shell.





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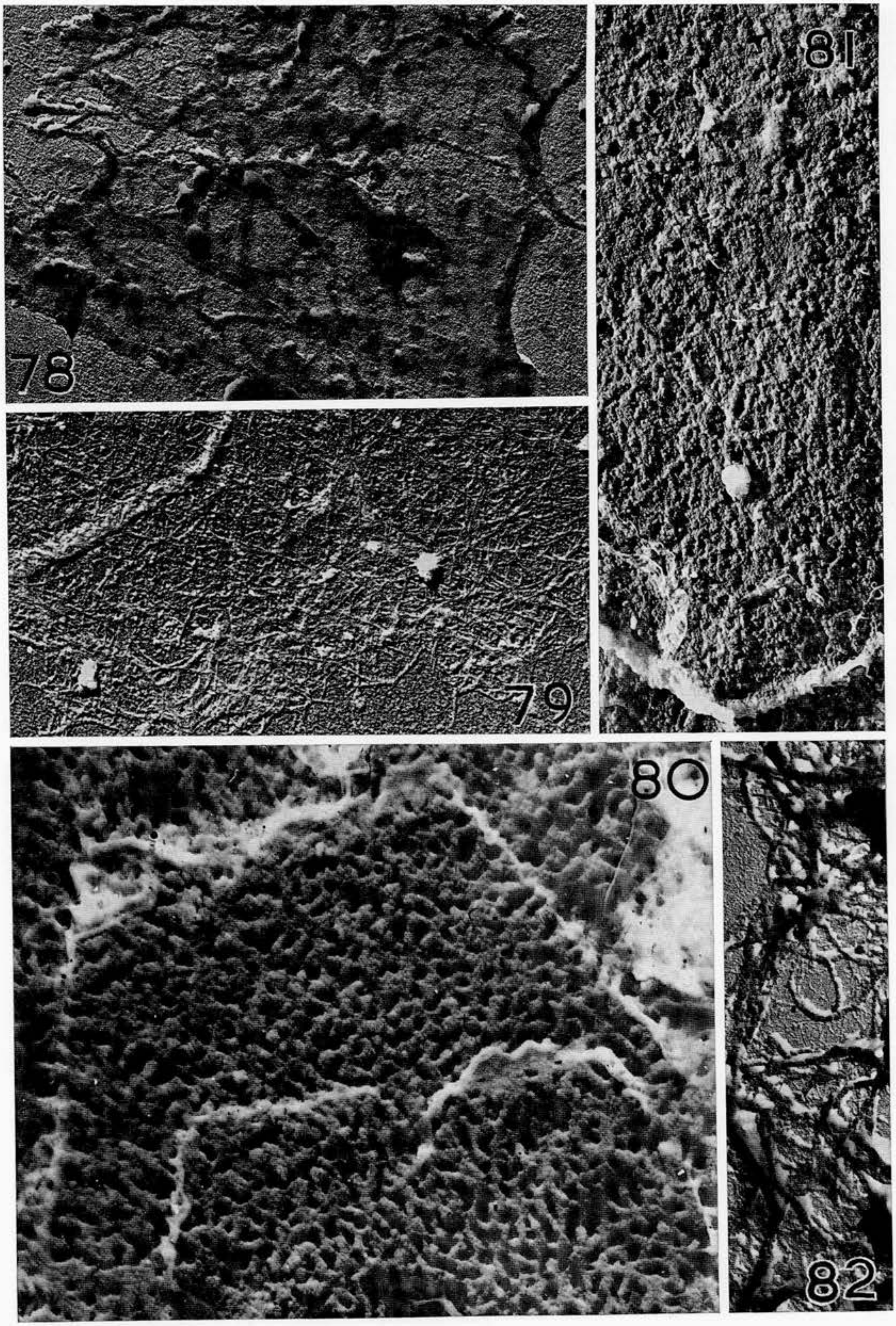

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